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THE OHIO JOURNAL OF SCIENCE

VOL. XXXV JANUARY, 1935 No. 1

THE LYCOPODIACEAE OF OHIO

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Toledo, Ohio

Since the publication of a map of the Lycopodiums of Ohio by Griggs[1] in 1913, there have been many more specimens collected, considerably extending the range of some species.

The present paper is a report based upon specimens in the Ohio State Herbarium, Field Museum Herbarium, and that of the author.

On the whole, with a few exceptions, the range of all the species of Lycopodium in the state follows very closely the phytogeographic regions as set by Schaffner. Of these regions, the most important for our purpose is the Allegheny Plateau in the eastern portion of the state, which is divided into three main parts.[2]

Of the seventy-one different localities in which one or more species of Lycopodium have been collected in Ohio, sixty-two are located in the Allegheny Plateau region, and they are about equally well distributed in both the glaciated and non-glaciated portions.

The nine remaining localities are scattered over the central and north-western sections of the state which are not located in the Allegheny Plateau.

Perhaps by careful searching where conditions are favorable, more localities can be found where Lycopodiums may be collected to still further extend the range of some species.

Let us now consider separately, each individual species found in Ohio.

Lycopodium lucidulum Michx. is perhaps the best known and most widely collected species in the state. Its occurrence is mainly on the

[1]Observations on the Geographical Composition of the Sugar Grove Flora, Griggs, 1913.

[2]Revised Catalog of Ohio Vascular Plants, Schaffner, 1932.

Allegheny Plateau, but it has been listed from Allen, Champaign, Clark, and Fulton counties.

Lycopodium porophilum, L. & U.—The typical habitat of this species is cool, shaded, sandstone cliffs such as one finds in the gorges and caves of Hocking county and it should be looked for wherever such conditions occur. It has never been collected in Ohio outside the Allegheny Plateau regions.

Lycopodium inundatum L.—This species does not confine itself to any one region, but grows wherever conditions are favorable, usually in wet, sandy places and is often associated with sphagnum moss. It has been collected in Knox, Portage and Trumbull counties and is frequently found in the Oak Openings of Lucas and Fulton counties.

Lycopodium obscurum L.—Fairly well distributed in the northern and southern Allegheny Plateau regions and is also very often found in the Oak Openings. I have not separated variety *dendroideum* (Michx.) D. C. Eaton.

Lycopodium clavatum L.—Known from nine counties in Ohio and entirely from the Allegheny Plateau regions. Several varieties of this species have been described but due to the fact that not many of the specimens studied had mature fruit, it was deemed advisable to treat them all under the specific name alone.

Lycopodium tristachyum Pursh.—This species is not as well known or as common as some, but once it is distinguished it is never mistaken for any other. In Ohio it has been collected from Ashtabula, Fairfield, Hocking, and Licking counties. The localities are all within the boundaries of the Allegheny Plateau.

Lycopodium complanatum L.—Next to *L. lucidulum*, this is the most widely collected species in the state and also is found only in the Allegheny Plateau regions.

Lycopodium complanatum, var. *flabelliforme* Fernald.—Only one specimen has so far been identified as being this variety. However, the difference is so slight that it may be easily overlooked. The specimen which I have was collected near Swanton, Fulton county, in 1925. During the summer of 1933 I visited the same locality but was unable to find it again.

KEY TO THE LYCOPODIUMS OF OHIO[3]

A. Sporophylls not different from foliage leaves, not in a terminal spike or strobilus.....B.
A. Sporophylls different from foliage leaves, in a terminal strobilus.....C.
B. Leaves broadest above middle, distinctly serrate; plants regularly, dichotomously branched.....*L. lucidulum*
B. Leaves sometimes broader at base, very slightly or not at all serrate; plants erect, dichotomous but branching more frequently.....*L. porophilum*
C. Sporophylls rather herbaceous.....*L. inundatum*
C. Sporophylls scale-like.....D.
D. Strobilus sessile, plant tree-like.....*L. obscurum*
D. Strobilus peduncled.....E.
E. Leaves linear, awl-shaped.....*L. clavatum*

[3]Key adapted from Wilson—Preliminary Reports on the Flora of Wisconsin, IV.

E. Leaves scale-like.....F.
F. Branches with constrictions.....G.
F. Branches without constrictions, fan-shaped, 1–3.5 mm. wide; ventral median leaves much reduced.....*L. complanatum* var. *flabelliforme*
G. Branches 1–1.5 mm. wide, rather squarish; ventral median leaf reaching or overlapping the one above; plant glaucous.....*L. tristachyum*
G. Branches 1–3 mm. wide, flattened; ventral median leaves much shortened, on the older branches not reaching the one above.....*L. complanatum*

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Prehistoric Chinese

Little did we think that when J. Gunnar Andersson went to China in 1914 as Advisor to the Chinese Government on Mining that twenty years later we would see him in the light of a discoverer of the first definite records of fossil man in Asia, north of the Himalayas. It is a far cry from the discovery and exploration of the Yen Tung Shan iron ores to the little cave some 37 miles southwest of Peiping which he heard contained "dragon bones." This cave, known as Chou K'ou Tien, yielded the now famous Pekin Man, so ably described by the late Davidson Black under the name **Sinanthropus pekinensis.** This discovery came about in a most natural way. Andersson had become interested in the well known Chinese medicine "Dragon Bones"; trailing down their source he found the deposits where they were preserved as fossils, finding there the first dinosaur from a definite locality. From that time on any deposits which contained dragon bones were searched. This lead him to the cave and the discovery of the Pekin Man.

In his eleven years of traveling in China, the loess, or as the Chinese call it, the Huang T'u (Yellow Earth), that great blanket of yellow earth which covers much of China, drew him to a study of what it had hidden away in its beds. Here he found below the loess some Paleolithic sites and at or near the top some Neolithic sites as well.

It is impossible to do justice to the great mass of information packed between the covers of this book in a review. As a geologist the author gives us a very complete summary of the geology of China for the regions he discusses. Included in this are his contributions and discoveries as well. The careful use of illustrations increases the usefulness of the book.

Our thanks to Professor Andersson for giving us a not too technical taste of the great amount of work that he was able to accomplish during his time in China. The publishers, too, have done their part well in giving us this interesting book on the ancient men of China.—WILLARD BERRY.

Children of the Yellow Earth. Studies in Prehistoric China, by J. Gunnar Andersson. Translated from the Swedish by Dr. E. Classen. 345 pp. New York: The Macmillan Co., 1934.

ECOLOGICAL OBSERVATIONS ON *AMBYSTOMA OPACUM*

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Several reports dealing with the life history of *Ambystoma opacum* Gravenhorst have appeared, among which are the works of Mann (1855), Deckert (1916), Dunn (1917), Brimley (1920), Bishop (1924), Lantz (1930), Noble and Brady (1930 and 1933). The species has been found in scattered areas over Ohio, but no previous studies concerning its breeding habits within the state have been published. In studying the ecology of certain upland forest areas in southwestern Ohio this species was encountered several times and its nesting sites located. The observations made to date seem to be of sufficient interest to justify this report. Physiological studies have been carried on in the laboratory as a means of further analyzing the conditions found in nature.

NESTING

Ambystoma opacum, in southwestern Ohio, inhabits what are known locally as "swamp forests." These forests are located on upland flats of impervious soil from which the water drains very slowly. The forests differ in their degree of development from the pin-oak to a nearly pure beech forest. Combinations of white elm, red maple, hickories and gums are found in the different stands. The herbaceous story is limited. Tree roots crowd to the surface, indicating a soil that is saturated with water a considerable portion of the year. In this type of environment I have found this salamander in Clinton county near Villar's Chapel, in Warren county along the earthworks at Fort Ancient and in an oak-hickory forest in the southwestern corner of the county, and in Clermont county near Goshen Station.

Adult salamanders are found most commonly in the months of September and October. The species is rarely met with at other times. Clues which led to the discovery of the nests were the finding of the larvae in certain pools in the spring of 1932 and 1933, and the observations of Noble and Brady

(1933). These authors state that "*Ambystoma opacum* lays its eggs under leaf mold, sphagnum, dry water weed or other cover in situations which will be flooded by the winter rains." Mann made the first observations on the breeding habits of this species at Gloucester C. H., Virginia, in 1854. He wrote the following description: "The localities are beds of small ponds in the woods, which in rainy seasons have water in them. . . . The nests . . . were in a small hollow in the surface of the earth, deeply covered with leaves, and under which were tunnels extending in all directions. In these hollows the animals were . . . curled up over their eggs." Not all parts of the wooded areas offer suitable breeding grounds, but only certain depressions, either natural or artificial, are chosen for the nests. Only one nest was found under an inverted half of a hollow log. All others were beneath leaf litter. Mouse or crayfish tunnels are utilized, but many nests show no connection with other excavations and must be made by the female salamander. The male has not been observed to have any part in nest building. The nests are readily found by turning the over-lying litter with a small hand rake. They measure three to four inches in diameter and are from one to two inches deep. The nests are usually not in the dampest part of the depression, but along the margins of the low banks or on a raised portion of the pool floor. Adequate cover is essential as a concentration of nests in the most favorable places shows. Some moisture is required, but as shown below too much water favors premature hatching.

The time of egg laying was not exactly determined, but chiefly occurred between September 27 and October 5. This was ascertained from the development of eggs laid in the laboratory by a female salamander collected October 6. This animal was placed in a box containing moist sand covered with moss. She hollowed out a small area beneath the moss and laid 81 eggs on October 8. Six days were required to reach the degree of development possessed by eggs collected October 10. With few exceptions all the eggs collected did not vary more than five days in their degree of development. Twenty-five nests were observed and counted. The average number of eggs was 98 per nest. Egg counts of individual nests were 120, 91, 85, 90, 80, 69, 155, 112, 87, 147, 73, 104, 89, 116, 69, 150, 116, 99, and 99. There was also one double nest with 174 eggs and a combination of four nests which averaged

84 eggs each. A second counting, 66 days after the first, was made on four nests in the field.

Nest Number	1	2	3	4
Number of eggs, October 13.....	147	69	87	155
Number of eggs, December 18.....	141	53	70	134

The average loss was slightly over 10%. Eggs which have failed to develop can be recognized by their discoloration. These were not included in the second counting. A number of the eggs are no doubt destroyed by beetles and centipedes which are common visitors in the nests.

In agreement with earlier writers and contrary to Noble and Brady (1933), I have always found the female on top of the eggs. Her tail may be curled or straight, but her body invariably rests on the egg clutch. The accompanying photograph shows this clearly. Variation in the length of time that the female stays with the eggs has been found. When the females are separated from the nests during the counting of the eggs they usually lie quietly on the leaf litter, making no effort to escape. After being returned to their nests they may or may not continue to brood the eggs. Four of seven females were found to be still brooding their nests after a temporary removal. One female was disturbed for photographing twice but stayed with her nest two weeks longer. Females were brooding undisturbed nests November 6, about one month after egg laying, but had left a month later, December 6. All females whose nests were disturbed left before November 6. The eggs have a coating of soil adhering to them. Since not all are in contact with the soil at one time it appears that the female must burrow through the eggs, changing their position. Her body is free from dirt. In deserted nests many of the eggs become matted together. Such clumps have a low percentage of development. Males are occasionally found in the nesting area after egg laying, but are usually scattered in the vicinity of the nesting grounds.

HATCHING

It was found that the growth of the embryo follows very closely the growth stages of *Ambystoma maculatum* as figured by R. G. Harrison (1925). Consequently the "Harrison

Stages" are used in recording the early growth of *Ambystoma opacum* larvae. Laboratory experiments were conducted to determine the percentage of eggs capable of hatching and the ages at which hatching occurs. From a total of 220 eggs immersed in water, 182, or 80% (Table I) hatched.

It was found that it is not always necessary for an egg to be immersed in water in order to hatch. After heavy rains, insufficient to flood the nest but moistening it, some larvae will hatch. This was observed in the field December 18 and again January 8. The larvae emerging under these conditions perish if the rainfall is insufficient to provide permanent inundation.

TABLE I

Hatching Experiments

All larvae except those in nest 3 were placed in fingerbowls in tap water in the laboratory. The eggs in number 3 rested in a depression made in tightly packed clay. These eggs were kept outdoors. Rains covered the eggs to a depth of one-half inch between October 27 and 30. Eighty of these 100 eggs hatched during the three days of exposure. Five more hatched during the following week.

Number of the Nest	1	2	3	4	5	6
Number of eggs	12	25	100	25	48	10
Number of larvae	11	19	85	13	48	9
Total days immersed	10	2	3	5	½	2
Harrison stage at hatching	42–3	42–4	44–6	42–6	.....	.....
Total length, mm	13	13	13–5	13–5	15–8	18
Temperature, degrees C	21	21	15	21	21	21
Date of hatching	Oct.20	Oct.20	Oct.27	Oct.30	Nov.23	Dec. 9

If the nests were located in the dampest part of the area, the first heavy rain would enable all the larvae to hatch. Subsequent drying would be fatal to the entire population. The habit of placing the nests beneath heavy leaf litter and at a slight elevation usually prevents such premature hatching, since most of the eggs do not hatch before permanent flooding occurs. The completion of hatching is attributed to the action of unicellular glands on the head, but in addition water must be absorbed before hatching can occur. The softening of the envelopes plus the wriggling movements of the larvae permit its escape. Either the head or the tail may emerge first. Larvae with the gelatin capsules still fastened over their heads are common sights.

The embryo is able to emerge from the gelatin by the time it has reached Harrison stage 42. Noble found larvae able to

hatch in a slightly less developed condition, stage 38 approximately. Two-thirds of the larvae used in the same experiment, however, hatched at a later stage comparable to the above. Eggs kept at low temperatures until past their normal hatching time were able to emerge when as young as stage 40. This

TABLE II

GROWTH OF LARVAE FROM EGGS LAID IN THE LABORATORY

Eighty-one eggs were laid in the laboratory October 8. October 10 only 11 showed embryological development. These were placed in a fingerbowl containing tap water at room temperature, and daily observations made.

DATE	HARRISON STAGE	TOTAL LENGTH, MM.	REMARKS
October 10.....	8–9	3 (D. of capsule)	11 living
October 11.....	21		11 living
October 12.....	27	4 (D. of capsule)	11 living.
October 13.....	31		8 living.
October 14.....	35		7 living.
October 16.....	37	5 (D. of capsule)	1 photographed.
October 18.....	39		
October 20.....	40		
October 23.....	42	12 total length	6 living.
October 27.....	43	12.5 total length	5 hatched Oct. 28–9.
November 3....	46	17 total length	pH of water 7.9.
November 10....	46 plus	18 total length	5 survivors.
November 17....	46 plus	18 total length	4th digit appeared.

TABLE III

GROWTH OF LARVAE SECURED FROM FORT ANCIENT

DATE	HARRISON STAGE	TOTAL LENGTH, MM.	REMARKS
October 10.....	35	8	These larvae were freed from the egg capsules at the beginning of the experiment. Six larvae were used. The water was kept at room temperature. Its pH was 7.9.
October 12.....	37	10.5	
October 14.....	40	13	
October 16.....	41	15	
October 18.....	44	16	
October 20.....	46	18	
October 23.....	46 plus	18	
October 27.....	46 plus	19	
November 3.....	46 plus	20	

degree of development may be accomplished in 15 days or may require two months, depending on the temperature. In order to learn the lowest temperature at which eggs of *Ambystoma opacum* might hatch, five sets of ten eggs each were placed in water at 21° C., 7°, 5°, and 2° C. After 12 hours immersion ten larvae had emerged from the eggs kept at 21° C., five from the set at 12°, two from the set at 7°, two from the set

at 5° C., none from the set at 2° C. Eggs were often kept in water in the Frigidaire at a temperature of 2° to 3° C. without hatching. Thus 5° C. appears to be the minimum temperature at which the eggs will hatch. Eggs from which the outer capsules have been removed often fail to hatch even though placed in a favorable medium. The remaining capsule swells decidedly, becoming even larger than the original complete egg. The digestive action of the glands is reduced so that hatching is delayed.

THE EFFECT OF THE ENVIRONMENT ON GROWTH

It is apparent that the gelatin capsules are a vital necessity for the early life of the embryo. If the eggs are immersed in water before they are sufficiently developed to hatch, the ability to hatch appears lessened. However, embryos as little advanced as Harrison stage 35 thrive better without their capsules. Larvae of this stage are able to swim actively upon mechanical release. Larvae described in Table III were 18 mm. in length and were in stage 46 on October 20, ten days after having been freed from their capsules. Eggs from the same collection and kept in the same environment with capsules intact hatched October 20. These larvae had attained a total length of 13 mm. and were in Harrison stage 42–3. In another experiment liberated larvae measured 20 mm. the day that eggs from the same nest and kept in the same fingerbowl hatched at a total length of 17 mm. With all other factors remaining constant, larvae that have been freed from their capsules after having reached stage 35 show a more rapid development than those with capsules intact.

In view of these observations it seemed that rapidity of growth might also be dependent upon a number of factors such as temperature, ability to move about and the food available after hatching. A Frigidaire and a laboratory room offered uniform environments in which to conduct experiments necessary to show the effects of these different conditions, (Table IV). Eggs from the same nest were used. All larvae showed a similar degree of development, Harrison stage 40, at the beginning of the experiment. Three groups of animals were used in each location. All were kept in the dark. In Experiment A, eggs with capsules intact were placed on damp soil. In B, eggs with capsules intact were placed in water. In C, larvae freed from their capsules were placed in water. The experiment was

TABLE IV

EXPERIMENTS SHOWING THE EFFECTS OF ENVIRONMENTAL FACTORS ON GROWTH. DURATION OF EXPERIMENT, 30 DAYS

ORIGINAL CONDITION OF LARVAE IN EXPERIMENTS A, B, AND C	EXPERIMENT A_1, FRIGIDAIRE TEMPERATURE 2° C.	EXPERIMENT A_2, LABORATORY TEMPERATURE 21° C.
Diameter of entire egg, 6 mm. Total length of larvae, 14–14.5 mm. Harrison stage 40. Fore limb bud undivided. No hind limb buds. Gills with few rami. Balancer present. Considerable yolk present.	10 eggs on water saturated soil. 6 survived, none hatched. Development: Total length, 14–14.5 mm. Harrison stage 40–41. Fore limb bud undivided. No hind limb buds. Gills with few rami. Balancer present. Little change in yolk content.	10 eggs on water saturated soil. 2 survived in the egg. 4 hatched on damp soil, perished. 4 perished in the egg. Development: Total length, 16 mm. Beyond Harrison stage 46. 4 digits on fore limb. Hind limb buds microscopic. Gill rami well developed. No balancers. More pigmented than A_1. Yolk practically exhausted.
HABITAT CONDITIONS, EXPERIMENT A		
Pint glass jars used as containers. Kept closed. Air practically saturated with water vapor. pH of soil in A_1, 5.6. pH of soil in A_2, 6.2.		
EXPERIMENT B, WATER ANALYSIS	EXPERIMENT B_1, FRIGIDAIRE	EXPERIMENT B_2, LABORATORY
Frigidaire / Laboratory pH..... 7.2 / 7.5 O_2, cc. per liter..... 9.00 / 5.82 Free CO_2, per liter.. 3.03 / 3.06 Fixed and half-bound CO_2 per liter..... 8.00 / 9.80	10 eggs entire, in 250 cc. tap water. 9 survived, none hatched. Development: Total length, 15 mm. Harrison stage 40–41. Fore limb buds undivided. No hind limb buds. Gill rami small. Balancers present. Possibly less yolk than in A_1.	5 eggs in 250 cc. tap water. 4 hatched within 24 hours. 3 larvae survived. 1 perished in the egg. Development: Total length, 18 mm. More advanced than Harrison stage 46. 4 digits on the fore limb. Hind limb buds microscopic. Gill rami well developed. No balancers. No yolk material remaining. Sise of head large in relation to body length, typical of starved larvae.

TABLE IV—Continued

EXPERIMENTS SHOWING THE EFFECTS OF ENVIRONMENTAL FACTORS ON GROWTH. DURATION OF EXPERIMENT, 30 DAYS

EXPERIMENT C, WATER ANALYSIS		EXPERIMENT C_1, FRIGIDAIRE TEMPERATURE 2° C.	EXPERIMENT C_2, LABORATORY TEMPERATURE 21° C.
	Frigidaire Laboratory		
pH.....	6.9 7.05	10 larvae freed from their capsules.	10 larvae freed from their capsules.
O_2, cc. per liter.....	7.79 4.49	Kept in 250 cc. tap water.	Kept in 3000 cc. tap water.
Free CO_2 per liter...	4.20 3.03	9 survived.	10 larvae survived.
Fixed and half-bound CO_2 per liter.....	7.59 5.09	Development: Almost identical to that in B_1. Total length, 15 mm. Harrison stage 40–41. Fore limb buds undivided. No hind limb buds. Gill rami small. Balancers present. Less yolk in gut than in B_1. Larvae lay inactively on the bottom most of the time.	Development: Total length, 19–20 mm. Considerably more advanced than Harrison stage 46. 4 digits on fore limb. Hind limb bud microscopic. Gill rami well developed. No balancers. Gut filled with food. Larvae active. Their gills show some evidence of cannibalism. These larvae the most advanced of all experimentals.

conducted for 30 days, at the end of which time all larvae were examined and measurements taken. In general, it was found that none of the animals kept in the Frigidaire showed appreciable development. A slight advantage might be accredited to group C over the others, but even this is too small to be significant. Marked differences were seen in the animals kept in the laboratory. In Experiment A_2, 40% of the larvae hatched on the wet soil. At no time were the eggs covered with water. The two survivors show a significantly greater growth than those kept in the colder temperature but with other factors constant. In Experiment B_2, where the larvae hatched almost immediately, the effect of temperature on the ability to hatch is seen. Eggs kept at 2° C. did not hatch. Also since no food was present the extent of growth was limited, although freedom of movement was possible. In Experiment C_2, the most favorable situation regarding temperature, food and freedom of movement were found. A larger quantity of water was necessary to prevent mutilation of gills and appendages by other larvae. These larvae outstripped all others in their growth, reaching a total length of 20 mm., with the development of appendages and other organs in proportion. The difference in development shown by the two groups of animals in Experiment B is influenced by the fact that in B_2 the larvae hatched almost immediately. That this increased growth was not due to freedom of movement alone is shown in Experiment B_1 and C_1 by the failure of larvae freed from their capsules to grow appreciably more than those confined within the egg membranes, kept at the same temperature and in the same volume of water. While the results of this experiment show no new phenomena, quantitative effects of such known factors as freedom of movement, temperature, presence of water and food in their relation to growth are definitely shown.

At the time of writing, February 5, 1934, conditions in the field are severe in respect to the survival of the eggs and larvae of *Ambystoma opacum*. At two breeding sites under observation partial flooding occurred January 5 and 8, so that apparently all the eggs hatched. Within the month all the water either froze solidly or evaporated, causing the death of the larvae. Some pools are still dry, and here a good proportion of the eggs are yet viable. Their fate depends upon sufficiently heavy and permanent rains in the weeks that follow.

SUMMARY

1. *Ambystoma opacum* is an inhabitant of the swamp forests of southwestern Ohio.

2. Its nests are located on the margins of depressions which are pools approximately six months of the year.

3. The average number of eggs in 25 nests was 98.

4. The females brood the nests for at least a month. They were always found with their bodies resting upon the eggs.

5. The early growth is very similar to that of *Ambystoma maculatum* and may be compared with the Harrison stages figured for that species.

6. While a definite stage must be reached before hatching can occur, this growth may be accomplished in as short a time as 15 days. Older larvae hatch at a slightly less advanced condition than younger larvae that have grown more rapidly.

7. Eggs were not able to hatch at 2° C., but four out of twenty hatched at 5° C. The highest percent hatched at room temperature, 21° C.

8. Embryos of Harrison stage 35, 8 mm. in length, removed from their egg capsules and placed in water grow more rapidly than those that have been retained within the capsules.

9. A low temperature, 2° C., and dessication retard the growth of the larvae, while freedom of movement at a higher temperature, 21° C., and presence of food, Copepods and Ostracods, favor their growth.

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EXPLANATION OF PLATE

Fig. 1. Female *Ambystoma opacum* brooding her nest. Warren County, October 21, 1933.

Fig. 2. Egg with outer capsules removed. Harrison stage 40, 8 mm. total length. 5 × natural size.

Fig. 3. A typical hatching stage, Harrison stage 45. Total length, 18 mm. Larvae from Fort Ancient, December 15, 1933. 5 × natural size.

Fig. 4. Experimental animals showing the effect of temperature on growth. The larger animal was kept at 21° C., the smaller at 2° C. Both were taken from the same nest and freed from their capsules at the beginning of the experiment. The larger larvae shows four digits on the fore limb, rudimentary hind limbs, no balancer present, gill rami well developed. The smaller one has the fore limb bud undivided, no hind limb bud, balancer present, gill rami small. Similar food was available to both animals. All other larvae of the same sets are identical with these figured. 5 × natural size.

Fig. 5. A more advanced larvae, kept in an aquarium at room temperature for two months after hatching. 4 × natural size.

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RESPONSE OF EUROPEAN CORN BORER[1] MOTHS TO COLORED LIGHTS

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INTRODUCTION

One of the most frequent questions and one of the most difficult to answer for those connected with corn borer research problems is that which concerns the phototactic responses of the adult or moth. The common impression that all insects are attracted to lights has led to the assumption that corn borer moths could be trapped in sufficient numbers to aid materially in the control of this pest. The fact that the moths are night fliers has further strengthened this assumption.

Because there was a general demand for definite information on this point, it was decided in 1926 to inaugurate investigations dealing with this phase of the problem. The data accumulated constitute the subject matter of the present discussion.

THE PROBLEM

Field and laboratory work was so outlined as to endeavor particularly *to determine the influence of lights of different colors on the behavior of the insects.*

MATERIALS AND EQUIPMENT

Description of Filters Used

Several filters, each 6½ inches square, were used in the colored light tests. These ray filters were manufactured by the Corning Glass Works, Corning, N. Y.

The code numbers for all of the filters have been changed since the work was started. Table I shows the wave-length, name, and number of the filters. It will be noted that the G34 and G24 used in these experiments have been subdivided, the visible transmission being determined by the position of the spectral cut-off. A brief description of each filter follows:

Pyrex.—This glass now known as Heat Resisting Clear Chemical Class No. 774 has medium ultra-violet transmission

[1] *Pyrausta nubilalis* Hubn.

and is highly transparent to visible radiation. The pyrex filter used in the tests transmitted light more freely than any other used; so the factor 1.0 was designated as the basal unit for calculating the transmission value of all the others.

Pale Blue Green.—This glass is now known as Light Shade Blue Green No. 428 and has the greatest ultra-violet transmission of any blue green glass available. It requires 9.61

TABLE I

Showing Filter Number with Present Name and Code Number*

Old Number	New Number	Wave Length
G86B	Discontinued—now H. R.† Clear Chemical Glass, No. 774	295–780
G38H	Noviol Shade C, No. 338	480–720
G38L	Noviol Shade O, No. 306	380–720
G34	Covers a series of glasses as follows H. R. Red Shade Yellow, No. 348. H. R. Lantern Shade, No. 349. H. R. Yellow Shade, No. 351.	525–780
G24	Covers a series of glasses as follows H. R. Signal Red, No. 243. H. R. Lantern Red, No. 244. H. R. Traffic Red, No. 245. H. R. Lighthouse Red, No. 246.	600–780
G124J	Discontinued—Now H. A. Green, No. 492	320–780
G584J	Light Shade Blue Green, No. 428	300–660
G585L	Blue Purple Ultra, No. 585	290–485
G586A	Red Purple Ultra, No. 597	300–420
G55A	Signal Purple, No. 555	300–560

*The above information was furnished by D. L. Killigrew, Aviation and Optical Division of the Corning Glass Works. The wave length data were calculated from Sayre (5).

†H. R.—Heat Resisting.

times as much light as does pyrex for producing transmitted light of equal intensity; therefore, the ratio of intensity is 9.61 to 1.

Noviol O.—This filter is used to absorb ultra-violet, to eliminate haze and thus improve visibility both in visual and photographic work, and, in general, as a selective ray filter. The ratio of intensity is 1.14 to 1.

Noviol C.—This glass is characterized by the sharp transition between high transmission and strong absorption and is used to absorb ultra-violet. The ratio of intensity is 1.41 to 1.

Heat Resisting Yellow.—The old G34 filter used in these experiments covers a series of glasses as follows: H. R. Red

Shade Yellow No. 348, H. R. Lantern Shade No. 349, and H. R. Yellow No. 351. These are low expansion, heat resisting glasses with a sharp spectral cut-off ranging from red orange to lemon yellow, depending upon the position of the spectral cut-off. The ratio of intensity is 1.25 to 1.

Blue Purple Ultra.—This filter transmits .365 μ ultra-violet, .405 μ violet, .435 μ blue, and extreme red beyond .72 μ. The ratio of intensity is 3.07 to 1.

Heat Absorbing.—The blue green glass of this filter is effective for obstructing the infra-red, although it is not well adapted for absorbing the visible rays. The ratio of intensity is 2.18 to 1.

Signal Purple.—Both ends of the spectrum are transmitted. The ratio of intensity is 10.5, placing it slightly lower than Pale Blue Green.

Red.—The old G24 filter used in these experiments covers a series of glasses as follows: H. R. Signal Red No. 243, Lantern Red No. 244, H. R. Traffic Red No. 245, and H. R. Lighthouse Red No. 246. Inasmuch as the type of glass has nearly complete transparency for the longer wave-lengths, the visible transmission is determined mostly by the position of the spectral cut-off. The ratio of intensity is 2.45 to 1.

Red Purple Ultra.—This glass transmits .365 μ ultra-violet freely, .405 μ violet, and extreme red at about .72 μ. This filter has the lowest light intensity of any used in the tests, its ratio being 47.6 to 1.

Bulbs

Clear electric light bulbs of the strengths 10, 15, 25, 50, and 100 watts manufactured by the Mazda National Lamp Works (General Electric Co.) were employed in all of the tests. The 10-watt bulbs were 115V S14 Mazda B; the 15-watt bulbs were 115V S17 Mazda B; the 25- and 50-watt were 115V mill type P19; and the 100-watt were 115V PS25 Mazda C. Except in the 15-watt bulb, in which the filament was mounted straight, the filament in all the other bulbs used was mounted in the form of a helix. The advantage of using a lamp of the latter type is that the light is emitted in a straight line and not at an angle. The brilliance of a coiled filament is greater than that of a straight filament, due to the lesser projected area and the reflections from the inside of the coil.

When 50-watt and 10-watt bulbs were used together, it was

evident that the filaments would not be even; so the lights were mounted on adjustable holders to insure centering and compensating for intensity.

Assembled Apparatus

The apparatus used was in the shape of an oblong, rectangular box, 66″ long, 7″ high, and 18″ wide. (See Figure 1.) Ten filters were mounted in frames on one side. Screen wire

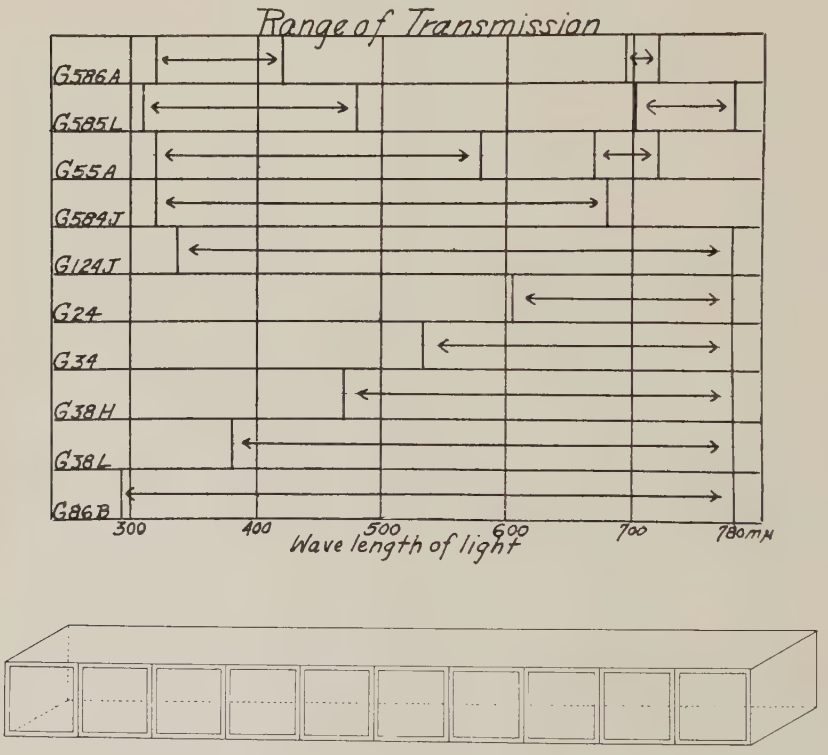


FIGURE 1

covered the top of the box, and a door in the wall opposite the filters permitted the introduction of the moths. The lights were arranged back of the filters on the outside of the test box and partitions separated them. The top was not covered.

The filters in this apparatus were arranged according to the way they are listed in Table II; that is, according to wave length. All of the calculations were made on the basis of 100. Thus Pyrex, the neutral glass, is placed in the center with the

filters having short wave-length on one side and those of longer wave-length than the pyrex on the other side, arranged in order of their wave-length. All lights were corrected for intensity.

TRANSMISSION DATA

The transmission data for the glass filters were obtained from the Bureau of Standards Technologic Papers by Coblentz and Emerson (1), Gibson and McNicholas (3), Gibson, Tyndall, and McNicholas (4), and Sayre (5). Gibson and McNicholas (3) present a chart and give instructions for converting these data which are for an equal energy spectrum. When the areas under the transmission curves were plotted on cross-

TABLE II

SHOWING RELATIVE DISTRIBUTION OF WAVE LENGTHS FOR CERTAIN FILTERS

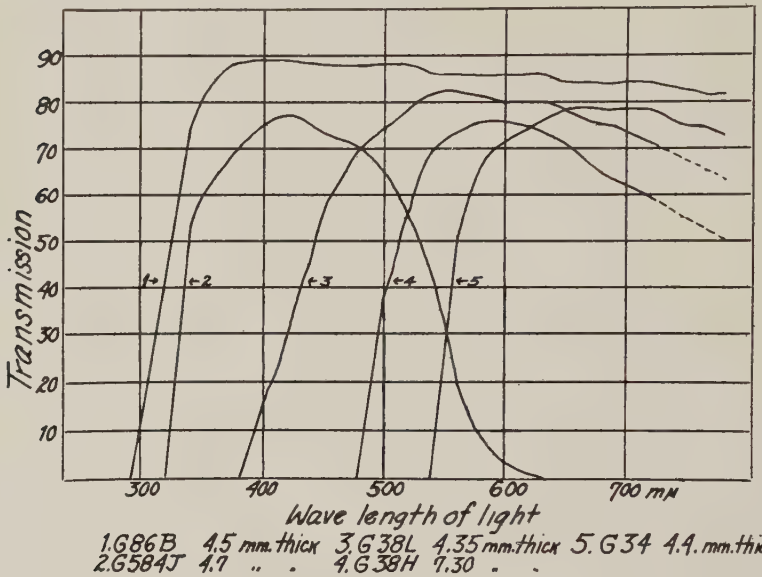
Filter	+ Short	— Short	Median	+ Long	— Long
Red Purple Ultra	63	16	.....	5	16
Pale Blue Green	22	27	27	22	.....
Signal Purple	28	35	28	5	4
Blue Purple Ultra	36	32	.....	.....	32
Pyrex	20	20	20	20	20
Heat Absorbing	14	23	23	23	18
Noviol O	5	25	25	25	20
Noviol C	.....	10	32	32	26
H. R. Yellow	.....	.....	27	41	32
Red	.....	.....	.....	53	47

section paper and compared, the percentage of total transmission for each filter was obtained. These data were calculated for a spectrum extending from 290 mμ to 780 mμ. (Fig. 1.) Gibson and McNicholas (3) give 770mμ as the limit of visible spectrum.

The transmission curves for the filters are shown in Fig. 2 and are applicable only for filters of the thickness indicated in each case. The transmission of a specimen, as stated by Gibson, Tyndall, and McNicholas (4), is that fraction of radiant energy incident on the first surface which gets through the second surface. In a comparison of the transmissions of different glasses, due account must be taken of the variation in thickness. It was not necessary to have the filters photographed and their range of spectrum calculated because the graphs given by the Bureau of Standards paper and by Sayre are sufficiently accurate for the filters used in this discussion.

RELATIVE SPECTRAL DISTRIBUTION OF RADIANT ENERGY

Each screen varied considerably in the amount of light energy that is transmitted. The percentage of energy from the light transmitted by each filter was found by calculation.



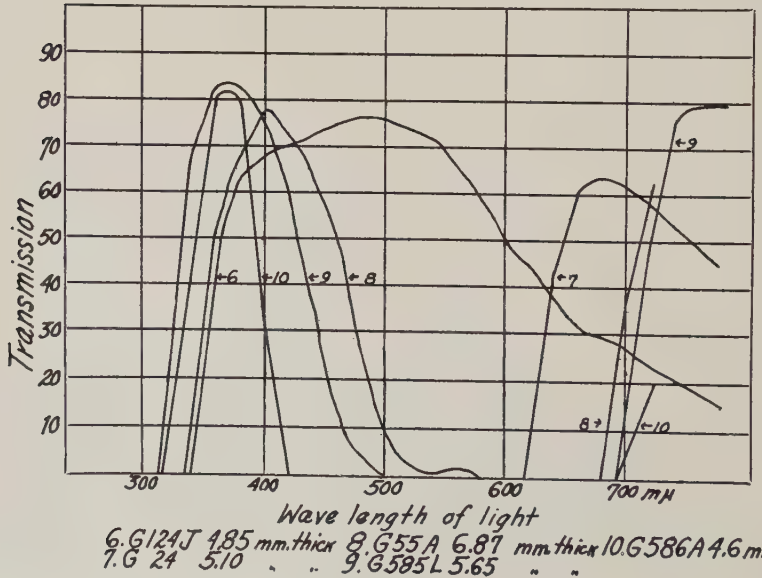


FIGURE 2

The data for the relative spectral distribution of radiant energy from 10-, 25-, and 50-watt Mazda B and 100-watt Mazda C bulbs were calculated from the curve given in General Electric bulletin Ld-114C. (7) (Figure 3.) The transmission value

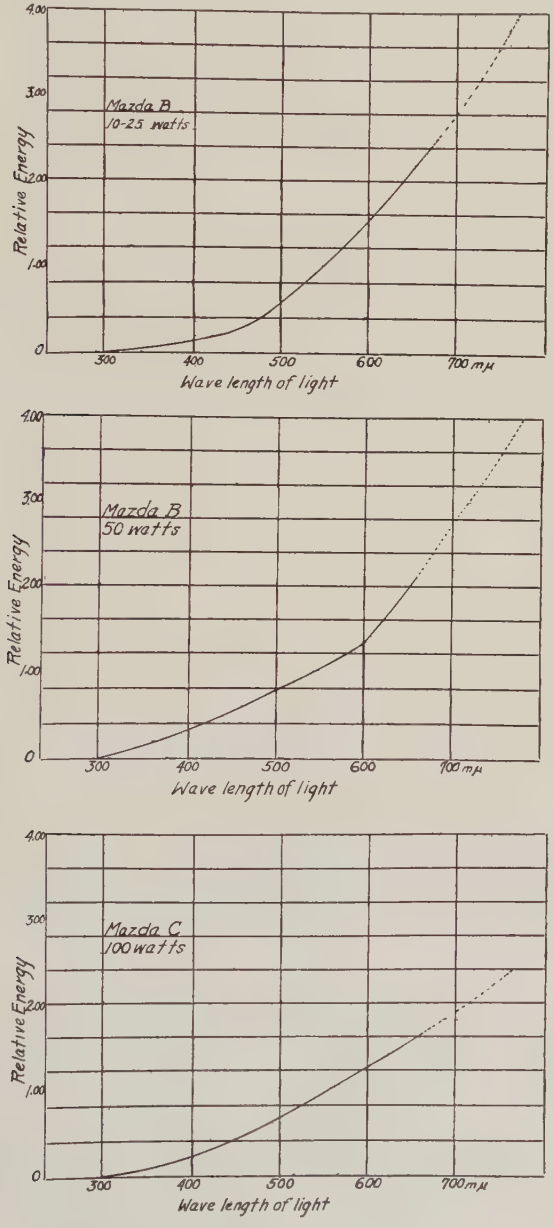


FIGURE 3

at each wave-length was multiplied by the values of relative spectral distribution of energy from the light. The areas under each curve were compared and reduced to percentages. The area of each curve thus measured is in proportion to the amount of light transmitted by a filter from bulbs of the same size placed at the same distance from the filter. These data are also applicable to Mazda lamps with inside frosted bulbs. In other words, the use of the frosted bulb does not introduce in the light output any factor that is not present in the clear glass bulb. The light is merely diffused and suffers a very small reduction in total quantity.

In a letter from General Electric Co., Harrison, N. J. (now Nela Park, Cleveland, Ohio), it was stated that "with the clear glass bulb it is apparent that the projected area of the light source; that is, the filament only, is small as compared to the projected area of the light source when an inside frosted bulb is used. In the latter case the entire bulb is considered as the source of light and hence its unit brilliancy is of a very much lower order than that encountered with the use of a clear bulb. In figures, the brilliancy of the inside frosted bulb is not over 2 per cent of that of a clear bulb."

SOURCE OF MOTHS USED IN THE WORK

All of the moths used in the laboratory tests were obtained from pupae which, as larvae, had spun up in corrugated paper strips. The paper strips containing the pupae were placed in large screen containers; the emerging moths were then collected from these and placed in smaller cages having a capacity of one hundred moths. The moths were kept for a period of 4 to 6 hours in a dark room of the same temperature and humidity as the one in which the light tests were conducted. The average temperature was 82° F. and the average humidity was 64 per cent. The boxes containing the moths were kept covered with damp cloths.

TECHNIQUE

Trial tests were conducted to determine the most satisfactory routine to be followed in introducing the moths into the light chamber. Lots of 100 moths each were placed in a compact wooden box with a screen wire cover. The sexes were kept separate. In some instances the moths were introduced at the end of the light chamber in which the short light waves

predominated; in other instances they were liberated in the end where the long light waves predominated; in still others they were released in the center of the box opposite the pyrex or neutral end.

The reactions of the moths were highly specific in that the insects introduced in the vicinity of the filters emitting light of short wave-lengths or in the center of the chamber opposite the neutral light exhibited a marked tendency to seek out the short wave-length lights. After a number of such trials it was finally decided that the most satisfactory point of introduction

TABLE III

SHOWING THE RESPONSE OF MALE EUROPEAN CORN BORER MOTHS TO COLORED LIGHTS

Replicates	Red Purple Ultra	Pale Blue Green	Signal Purple	Blue Purple Ultra	Pyrex	Heat Absorbing	Noviol O	Noviol C	H. R. Yellow	Red	Total
1	25	18	7	3	8	2	1	1	1	0	65
2	14	10	10	5	6	1	0	2	2	0	51
3	13	17	4	4	4	1	0	0	0	0	43
4	22	15	12	4	2	1	0	0	0	0	56
5	23	12	7	5	3	1	0	0	0	1	52
6	13	8	11	2	4	3	4	0	0	1	46
7	8	12	18	3	3	0	0	0	0	0	44
8	11	8	10	5	5	2	2	2	2	0	45
9	4	9	5	3	6	2	1	1	1	0	32
10	30	14	12	6	5	2	1	0	0	3	73
11	19	14	14	5	7	3	2	1	1	1	67
12	7	7	10	9	8	4	0	0	0	0	45
Total	189	144	120	54	61	22	11	7	5	6	619
Mean	15.8	12.0	10.0	4.5	5.0	1.8	0.9	0.6	0.4	0.5	

was in the center of the cage opposite the Pyrex or neutral light. It is possible, however, that this procedure may have unduly influenced the number of insects going to Pyrex, since a study of Tables III and IV shows a slightly larger number of moths attracted to Pyrex than to the theoretically more attractive and immediately adjoining light, Blue Purple Ultra. Moreover, the difference in the number of moths selecting Pyrex and those selecting the adjoining, less attractive Heat Absorbing was greater than theoretically would have been expected.

The tests were replicated many times, and before each trial the entire apparatus was carefully checked in order that the

same adjustment obtained for all tests. The lights in the room, except those connected with the apparatus, were extinguished while each test was in progress.

At the outset, it was not known how much time should be allowed the moths to complete their response. After a number of trials it was found that if the insects were given 20 minutes in which to adjust themselves, little change in position occurred thereafter; hence this period was used as the interval allowed for response throughout the work.

TABLE IV

SHOWING THE RESPONSE OF FEMALE EUROPEAN CORN BORER MOTHS TO COLORED LIGHTS

Replicates	Red Purple Ultra	Pale Blue Green	Signal Purple	Blue Purple Ultra	Pyrex	Heat Absorbing	Noviol O	Noviol C	H. R. Yellow	Red	Total
1	17	22	6	4	6	6	0	0	0	0	61
2	12	11	8	7	6	2	1	0	1	0	48
3	22	11	9	7	6	1	1	1	0	0	58
4	22	16	8	3	4	0	0	0	1	1	55
5	21	17	8	3	6	0	0	0	0	0	55
6	16	11	7	5	4	2	0	0	0	0	45
7	7	14	9	5	5	2	1	3	0	0	46
8	10	12	6	4	4	1	0	0	1	0	38
9	11	11	10	7	8	3	1	2	0	0	53
10	11	9	7	6	7	2	0	0	0	1	43
11	16	12	10	6	13	1	2	2	0	1	63
12	6	11	5	6	4	2	1	0	0	2	37
Total	171	157	93	63	73	22	7	8	3	5	602
Mean	14.3	13.1	7.8	5.3	6.1	1.8	0.6	0.7	0.3	0.4	

After the moths had once selected a light chamber, they were not easily disturbed, even though at the conclusion of an experiment the colored lights were extinguished and the room lights turned on directly above the apparatus.

RECORDED RESPONSES OF MOTHS AND ANALYSIS THEREOF

A study of Tables III and IV reveals the fact that the moths respond to the colors in order of their descending wavelengths. Reference to Table II shows that Red Purple Ultra has 63% of its transmission in the short + end, 16% in short −, nothing transmitted in the median, 5% in long+, and 16% in long −. This is in accordance with the description of the

filter which states that it transmits .365 μ ultra-violet freely, .405 μ violet, and extreme red at about .72 μ. Pale Blue Green was very close to Red Purple Ultra in order of response, which may be explained by reason of Pale Blue Green transmitting farther into the ultra-violet than any other blue green glass available. There is a marked difference from these on down in the table. Signal Purple transmits 5% in long + as compared with Pale Blue Green 22%, but this is offset by a transmission in long −. Blue Purple Ultra has 36% transmission in short +, 32% in short −, and 32% in long −, which corresponds to its description as transmitting .365 μ ultra-violet, .405 μ violet, .435 μ blue, and extreme red beyond .72 μ. There is a sharp drop in response from Pyrex to Heat Absorbing. Noviol O, Noviol C, H. R. Yellow, and Red are about equal in order of response to the moths. Owing to the small numbers of moths responding, no explanation is offered for the fact that Red receives more moths than H. R. Yellow.

According to Fisher's (2) method of analysis of variance, there are significant differences in response of moths to wave length. In Tables II and III the means are given under each total. Using Fisher's table (where $t = \frac{(n_1 + 1) + (n_2 + 1)}{(n_1 + 1) + (n_2 + 1)}$) a difference of 2.805 for Table II must exist between the succeeding differences of the means of the response of male moths to wave-length before they are significant. Thus, for example, there is a difference of 3.8 between Red Purple Ultra and Pale Blue Green; hence, this difference is significant. In Table III the difference is 2.04, and for the combined male and female is 3.995.

CONCLUSIONS

When the filters were arranged in the apparatus in the ascending or descending order of wave-length, and the light transmitted through the filters was in all instances of uniform or comparable intensity, the moths responded in significantly greater numbers to the lights of short wave-length than to those of long wave-length; that is, the blue light of the series attracted more moths than did the red light on the opposite end of the series.

at each wave-length was multiplied by the values of relative spectral distribution of energy from the light. The areas under each curve were compared and reduced to percentages. The area of each curve thus measured is in proportion to the amount of light transmitted by a filter from bulbs of the same size placed at the same distance from the filter. These data are also applicable to Mazda lamps with inside frosted bulbs. In other words, the use of the frosted bulb does not introduce in the light output any factor that is not present in the clear glass bulb. The light is merely diffused and suffers a very small reduction in total quantity.

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SOURCE OF MOTHS USED IN THE WORK

All of the moths used in the laboratory tests were obtained from pupae which, as larvae, had spun up in corrugated paper strips. The paper strips containing the pupae were placed in large screen containers; the emerging moths were then collected from these and placed in smaller cages having a capacity of one hundred moths. The moths were kept for a period of 4 to 6 hours in a dark room of the same temperature and humidity as the one in which the light tests were conducted. The average temperature was 82° F. and the average humidity was 64 per cent. The boxes containing the moths were kept covered with damp cloths.

TECHNIQUE

Trial tests were conducted to determine the most satisfactory routine to be followed in introducing the moths into the light chamber. Lots of 100 moths each were placed in a compact wooden box with a screen wire cover. The sexes were kept separate. In some instances the moths were introduced at the end of the light chamber in which the short light waves

predominated; in other instances they were liberated in the end where the long light waves predominated; in still others they were released in the center of the box opposite the pyrex or neutral end.

The reactions of the moths were highly specific in that the insects introduced in the vicinity of the filters emitting light of short wave-lengths or in the center of the chamber opposite the neutral light exhibited a marked tendency to seek out the short wave-length lights. After a number of such trials it was finally decided that the most satisfactory point of introduction

TABLE III

SHOWING THE RESPONSE OF MALE EUROPEAN CORN BORER MOTHS TO COLORED LIGHTS

Replicates	Red Purple Ultra	Pale Blue Green	Signal Purple	Blue Purple Ultra	Pyrex	Heat Absorbing	Noviol O	Noviol C	H. R. Yellow	Red	Total
1	25	18	7	3	8	2	1	1	1	0	65
2	14	10	10	5	6	1	0	2	2	0	51
3	13	17	4	4	4	1	0	0	0	0	43
4	22	15	12	4	2	1	0	0	0	0	56
5	23	12	7	5	3	1	0	0	0	1	52
6	13	8	11	2	4	3	4	0	0	1	46
7	8	12	18	3	3	0	0	0	0	0	44
8	11	8	10	5	5	2	2	2	2	0	45
9	4	9	5	3	6	2	1	1	1	0	32
10	30	14	12	6	5	2	1	0	0	3	73
11	19	14	14	5	7	3	2	1	1	1	67
12	7	7	10	9	8	4	0	0	0	0	45
Total	189	144	120	54	61	22	11	7	5	6	619
Mean	15.8	12.0	10.0	4.5	5.0	1.8	0.9	0.6	0.4	0.5	

was in the center of the cage opposite the Pyrex or neutral light. It is possible, however, that this procedure may have unduly influenced the number of insects going to Pyrex, since a study of Tables III and IV shows a slightly larger number of moths attracted to Pyrex than to the theoretically more attractive and immediately adjoining light, Blue Purple Ultra. Moreover, the difference in the number of moths selecting Pyrex and those selecting the adjoining, less attractive Heat Absorbing was greater than theoretically would have been expected.

The tests were replicated many times, and before each trial the entire apparatus was carefully checked in order that the

Grove, California, August 17, 1930, both collected by the senior author. Male holotype from Pacific Grove, California, in author's collection. Collected from Pine in these localities.

Empoasca convergens n. sp.

Resembling *fabae* in general appearance and coloration, slightly smaller and with distinct genitalia. Length, 3 mm.

Vertex about one-fourth wider between eyes than length at middle.

Color.—Pale green with variable markings, usually with a row of pale spots along anterior margin of pronotum.

Genitalia.—Male plates long and narrow, apices pointed. Of the male genital pieces, the lateral processes of the pygofers are rather long, stout, in ventral view, narrowed and pointed at apices with apical third rather strongly convergent. In lateral view they appear heavy, almost straight, with apex rather abruptly pointed. Dorsal spine consisting of two parts; the basal portion is broad and directed caudally and slightly ventrally. The apical portion is a long rounded, pointed spur which extends at right angles from the ventral apical portion of the basal part.

Described from a male and female specimen from Newaygo, Canada, April 22 and August 20, 1929, and three male and one female specimens from Toronto, Canada, September 1, 1929, tand a series of five male and one female specimens collected a Cedar Swamp, Ohio, by J. S. Caldwell, April 17, 1934. Male holotype and female allotype from Cedar Swamp, Ohio.

Empoasca dentata n. sp.

A small green species resembling *erigeron* in general appearance, but with distinct genitalia. Length, 3 mm.

Vertex bluntly produced more than one-half its length before anterior margins of eyes, almost twice as wide between eyes as length at middle.

Color.—Pale green to yellow, three dashes on basal portion of vertex and three spots on anterior margin of pronotum pale.

Genitalia.—Female last ventral segment produced and rounded. Male plates rather narrow, and covered with long hairs. Of the male genital pieces the lateral processes are long and narrow in ventral view with apices turned sharply outwardly and with rounded teeth-like processes on outer margins just before apices. In lateral view with apex slightly indented on upper margin. Dorsal spine broad, strongly curved anteriorly near middle, then narrowed to a pointed apex which is directed anteriorly and ventrally.

Described from a series of three male and two female specimens from Manhattan, Kansas, May 17, 1929, collected by D. A. Wilber, one male specimen from Douglas County, Kansas, at light trap, July 20, 1930, and one male from Cherokee County, Kansas, collected by Dr. R. H. Beamer. Male holotype and female allotype from Manhattan, Kansas.

Empoasca constricta n. sp.

Resembling *E. fabae* in general appearance, pale green with paler dashes and spots on head and pronotum. Length, 3 mm.

Vertex bluntly angularly produced, about one-fourth wider between eyes than length at middle.

Color.—Pale green washed with yellow, vertex with a median stripe and two oblique yellowish basal stripes. Pronotum with three pale spots on anterior margin. Wings greenish yellow, subhyaline.

Genitalia.—Female last ventral segment long, almost truncate. Male plates long and narrow. Of the male genital pieces the lateral processes are almost straight in lateral view with the upper margin concavely indented at apex, forming a finger process curved upwardly. In ventral view appearing constricted about one-fourth the distance from apex and with a pointed tip. Dorsal spine broad at base, rapidly narrowed then produced and strongly curved ventrally and anteriorly.

Described from a series of four male and four female specimens from Riley County, Kansas, collected in August and October; three male and two female specimens from Branford, Florida, July 31, 1930, and one male from Huachuca Mountains, Arizona, August 2, 1927, all collected by R. H. Beamer; also two male and two female specimens from Columbus, Ohio, September 15, 1898, and April 4, 1899, and one specimen from Gainesville, Florida, July 7, 1918 (C. J. Drake), all in Herbert Osborn collection.

Male holotype and female allotype from Columbus, Ohio; male and female paratypes from the above specified localities.

Empoasca diverta n. sp.

In general appearance and coloration resembling *pallidula* but with distinct genitalia. Length, 3 mm.

Vertex bluntly rounded, about one-fourth wider between eyes than length at middle.

Color.—Vertex brownish with pale markings. Pronotum and scutellum with a median pale area. Wings pale, veins white margined, with areas on corium broadly white.

Genitalia.—Last ventral segment with posterior margin roundly produced. Male plates broad at base, long with sharp points. Of the male genital pieces the lateral processes of the pygofers in ventral view are rather broad and directed inwardly and meet near the apices which are sharply curved outwardly and pointed. In lateral view the processes are slightly narrowed apically. Dorsal spine rather long, strongly curved anteriorly near its middle, narrowed and directed downwardly and ventrally.

Described from a series of four male and nine female specimens collected at S. Catalina Mountains, Arizona, April 25, 1926, by A. A. Nichol. The male is designated as the holotype.

Empoasca arta n. sp.

A small green species of the *fabae* type, but with more pointed head and distinct genitalia. Length, 3–3.5 mm.

Vertex bluntly pointed, one-fourth wider between eyes than length at middle. Pronotum almost twice as broad as median length.

Color.—Green washed with yellow, three basal pale lines on vertex; pronotum with three pale spots on anterior margin.

Genitalia.—Male long and slender. Of the male genital pieces the lateral processes of the pygofers are broad in ventral view, abruptly narrowed on outer margin near apex to form slender tips on inner margin. In lateral view with tips concavely excavated forming a finger process which is curved upwardly. Dorsal spine long and rather narrow, basal portion broad, strongly curved ventrally and anteriorly.

Described from one male specimen from Knight's Landing, California, collected August 22, 1930, by the senior author; one male specimen from Carson City, Nevada, August 9, 1929, and one male from Giant Forest, California, July 28, 1929, both collected by R. H. Beamer. The specimen from Knight's Landing is designated as the male holotype.

Empoasca occidentalis n. sp.

A banded species with angled head and with distinct genitalia. Length, 3–3.5 mm.

Vertex strongly angled, produced about one-half its length before anterior margins of eyes, about one-third wider between eyes than length at middle.

Color.—Pale green with bright green and smoky markings on vertex, pronotum and wings. Vertex usually with a pair of bright green markings on disc. Pronotum and scutellum smoky. A smoky green band across center of clavus and apex of wings. Anterior portion of clavus and area in front of anteapical cells pale, giving a banded appearance.

Genitalia.—Female last ventral segment with posterior margin produced, central fourth with a shallow square-shaped notch at center. Male plates short, appearing triangular. Of the male genital pieces the lateral processes in ventral view are strongly curved inwardly near tips. In lateral view these processes are almost straight. The dorsal spine is short and broad, slightly indented on inner margin, forming a sharp pointed process on inner ventral angle.

Described from a series of 48 specimens collected from Juniper at Twin Falls, Idaho, along the Snake River, in June, 1930; and one specimen from Donner Lake, California, August 6, 1930; two male and two female specimens from General Grant Park, August 12, 1930, all collected by the senior author. One male from Fish Lake, Utah, September 2, 1930; two male and three female specimens from Pingree Park, Colorado,

August 22, 1929, were collected by D. A. Wilber. Two male and two female specimens from Colfax County, New Mexico, August 21, 1927, collected by P. A. Readio and L. D. Anderson, and one male and three female specimens from Socorro County, New Mexico, August 18, 1927, collected by L. D. Anderson. Holotype male and allotype female from General Grant National Park, California.

Empoasca decora n. sp.

Resembling *aspersa* in size, coloration and general appearance. Length, 2.5–3 mm.

Vertex bluntly produced, about twice as wide between eyes as length at middle.

Color as in *aspersa*. Vertex, pronotum, and scutellum, pale green with irregular markings. Wings pale green to white, rather uniformly mottled with smoky areas. Veins pale to white.

Genitalia.—Female last ventral segment with posterior margin broadly roundedly produced. Male plates rather long, appearing pointed, set with heavy spines. Of the male genital pieces the styles are short, curved strongly inwardly and with tips divergent. Lateral process of pygofers rather heavy in ventral view. In lateral view appearing strongly curved dorsally on apical third and slightly narrowed. Dorsal spine rather short, broad tipped, and curved slightly anteriorly.

Described from a series of five male and five female specimens from Alpine, California, collected July 9, 1929; three male and three female specimens from Cedar City, Utah, collected August 19, 1926; one male specimen collected at Carson City, Nevada, August 9, 1929; and two male specimens from Alpine, California, collected July 9, 1929. All of the above specimens were collected by R. H. Beamer. A series of three male and four female specimens from Otera County, New Mexico, collected June 19, 1929, by Dr. R. H. Painter.

Holotype male and allotype female from New Mexico. Paratypes from localities mentioned above.

Empoasca venusta n. sp.

A pale yellow or green species without definite markings, resembling *fabae* in size and general appearance. Length, 3–3.5 mm.

Vertex about one-half wider between eyes than length at middle, bluntly rounded on anterior margin, not produced half its length before anterior margins of eyes.

Color.—Pale to bright green washed with yellow.

Genitalia.—Female last ventral segment produced on posterior margin. Male plates rather short and narrow at apex. Of the male genital pieces the styles are rather short and divergent at apex. Lateral processes of pygofers long in ventral view, with an abrupt bending outwardly, then inwardly, near apex with apices thin, slightly divergent

and curved outwardly. In lateral view appearing straight with pointed apices. The dorsal spines are short and broad with small pointed spur on the ventral anterior portion, entire spine slightly curved anteriorly.

Described from two male and two female specimens from Hocking County, Ohio, collected in September and October, 1933, by Dorothy M. Johnson. Male holotype and female allotype from Hocking County, Ohio.

Empoasca falca n. sp.

A blunt-headed species with slight banding. Length, 3.5 mm.

Vertex bluntly pointed, about one-third wider between eyes than length at middle, produced about one-half its length before anterior margins of eyes.

Color.—Vertex and pronotum brownish to yellow, wings greenish subhyaline with a faint smoky band across middle of clavus and another across apex of wings.

Genitalia.—Female last ventral segment with margin broadly produced. Male plates broad and rather short, appearing pointed at tips. Of the male genital pieces the oedagus is inflated on the apical half, the lateral processes of the pygofers rather short, in lateral view with apex narrowed and produced in a setaceous process. In ventral view the inner margins are concavely curved at the apex, forming finger processes on outer margin. Dorsal spines rather long, directed ventrally and anteriorly and gradually narrowed to a sharp point.

Described from two male and two female specimens, collected at Yosemite Park, California, August 10, 1930, by the senior author. Male holotype and female allotype in author's collection.

Empoasca plebeia n. sp.

Resembling *bifurcata* in general appearance, but with distinct genital characters. Length, 3 mm.

Vertex angularly produced, one-third wider between eyes than length at middle.

Color.—Green without definite markings. Wings greenish subhyaline.

Genitalia.—Male plates long and narrow with upturned tips. Of the male genital pieces the lateral processes are long and slender. In ventral view they form slender curved finger processes on outer margins curving inwardly. In lateral view these are constricted near apex and produced as slender tips. Oedagus long, extending more caudally than dorsally, and with a long finger process arising ventrally about half its length and curving caudally and dorsally. Dorsal spine broad and short, directed ventrally and slightly caudally, with a blunt apex.

Described from a series of fifty male and female specimens collected at Belle Glade, Florida, summer of 1929, by Hugh Clifton; a series of twenty-two specimens from Sanford, Florida,

taken at trap light, August 9, 1929, by C. O. Bare; a male specimen from Everglade, Florida, August 11, 1930, collected by Paul Oman; and a male specimen from Maricopa County, Arizona, August 7, 1927, collected by R. H. Beamer, and a series of male and female specimens in Ball collection from Port-au-Prince, Haiti.

Holotype male and allotype female are from Belle Glade, Florida.

Empoasca torqua n. sp.

Resembling *fabae* in general appearance, but with distinct genitalia. Length, 3 mm.

Vertex roundedly produced as in *fabae*, one-third wider between eyes than length at middle.

Color.—Green washed with yellow, vertex with white markings, three large spots on anterior margin of pronotum with central portion of scutellum white. Wings greenish, hyaline, unmarked.

Genitalia.—Male plate rather long and pointed, triangular. Of the male genital pieces the lateral processes of the pygofers are rather short, slender, and with short pointed apices. Styles short, curving outwardly. Dorsal spines broad at base, rapidly narrowed to rather long curved apical portion which is directed inwardly and curved upon itself.

Described from a series of four male specimens collected at Meridian, Mississippi, July 17, 1930, by R. H. Beamer; a series of six males collected in Champaign County, Ohio, in April, 1934, by J. S. Caldwell, and one male specimen collected at Vienna, Illinois, June 14, 1934, by H. H. Ross and the senior author. Male holotype and paratypes in author's collection. Paratype males in Kansas University Collection and Illinois Natural History Survey Collection.

Empoasca unca n. sp.

Size and general appearance of *fabae*, but with head more produced and genitalia distinct. Length 3–3.5 mm.

Vertex almost one-third wider between eyes than length at middle, bluntly angled, produced about one-third its length before anterior margin of eyes. Wings long and narrow.

Color.—Pale green, vertex, pronotum, and scutellum tinged with orange, a median basal spot on vertex, three spots on anterior margin of pronotum, and a pale median stripe on scutellum. Wing subhyaline, veins green.

Genitalia.—Male plates rather short, appearing triangular but with tips turned upward and curved. Of the male genital pieces the lateral processes of the pygofers are short and rather broad, in ventral view appearing notched on inner margin at apex, forming a sharply curved finger process pointing inwardly. In lateral view appearing slightly indented on upper margin at apex. Dorsal spine broad and short,

caudal margin strongly convexly rounded, ventral anterior corner produced into a short sharp spur-like process.

Described from one male specimen collected at Emery, Utah, August 16, 1929, and two males from Grand Canyon, Arizona, August 11, 1927, all collected by R. H. Beamer. Holotype male from Grand Canyon, Arizona. Male paratypes from Grand Canyon and Emery, Utah.

Empoasca ratio n. sp.

Resembling *birdii* in color and general appearance but with distinct genital characters. Length, 3.5 mm.

Vertex about one-fifth wider between eyes than length at middle. Wings long, considerably produced beyond abdomen.

Color quite variable. Some specimens are green with few or faint markings. In well marked specimens the ground color is pale green or yellowish, marked with dark brown on pronotum and scutellum, and basal half and apical third of wings. Usually three elongated pale spots on posterior half of vertex and three on anterior margin of pronotum.

Genitalia.—Female last ventral segment with posterior margin roundedly produced. Male plates triangular, appearing to have pointed tips. Of the male genital pieces the lateral processes of the pygofers are stout in ventral view, gradually tapering to pointed slightly divergent apices. In lateral view gradually curved upwardly and with pointed apex. Dorsal spine broad and rather short, directed ventrally and notched anteriorly near apex and somewhat ventrally, forming a ventral anterior process which is directed anteriorly and curved ventrally.

Described from a series of three male and four female specimens collected at Republic, Washington, August 6, 1931, by R. H. Beamer. Male holotype and female allotype in Kansas University Collection.

Empoasca dilitara n. sp.

A pale green species with orange yellow vertex and without definite color markings. Length, 2.5–3 mm.

Vertex one-fourth wider between eyes than length at middle, rounded in front, produced about one-third its length before anterior margins of eyes.

Color.—Vertex orange yellow, pronotum green, scutellum pale yellow, wings greenish yellow, subhyaline.

Genitalia.—Female last ventral segment roundingly produced. Male plates long and slender. Of the male genital pieces the styles are long and slender with tips divergent. The lateral processes of the pygofers are long and in ventral view straight on the inner margin. The outer margin curved outwardly to near tip where it rapidly narrows to a pointed apex. In lateral view the apex is constricted ventrally, forming a dorsal finger process. Oedagus in lateral view with posterior process extending dorsally at about the middle. Dorsal spine triangular, not curved, extending ventrally and with tip bending inward.

Described from a male and two female specimens collected in Eddy County, New Mexico, June 17, 1929, by Dr. R. H. Painter. The male is designated as the holotype and the female as the allotype.

Empoasca simplex n. sp.

Resembling *pergandei* in size and general appearance but with distinct genitalia. Length, 3.5 mm.

Vertex broadly rounded, scarcely produced before anterior margins of the eyes, about twice as wide between eyes as length at middle.

Color.—Vertex yellowish, pronotum, scutellum, and wings green tinged with yellow.

Genitalia.—Female last ventral segment with posterior margins produced, slightly emarginate at middle with indications of about three small teeth. Male plates long and narrow. Of the male genital pieces the lateral processes in ventral view are long, rather heavy, with tips slightly narrowed and convergent. In lateral view the processes are curved upward near the apices and are sharp pointed. The dorsal spine is rather heavy, somewhat strongly curved on anterior margin forming a rather short thick terminal process which is directed ventrally and slightly anteriorly.

Described from two male specimens from Shoshone Basin, Idaho, collected July 27, 1930, and one male from Blackfoot, Idaho, collected June 26, 1930, by the senior author; one male from Burns, Oregon, collected August 3, 1927, by R. H. Beamer and two specimens from Harper County, Kansas, June 22, 1929, collected by D. A. Wilber. Male holotype from Shoshone Basin, Idaho, in author's collection.

Empoasca similis n. sp.

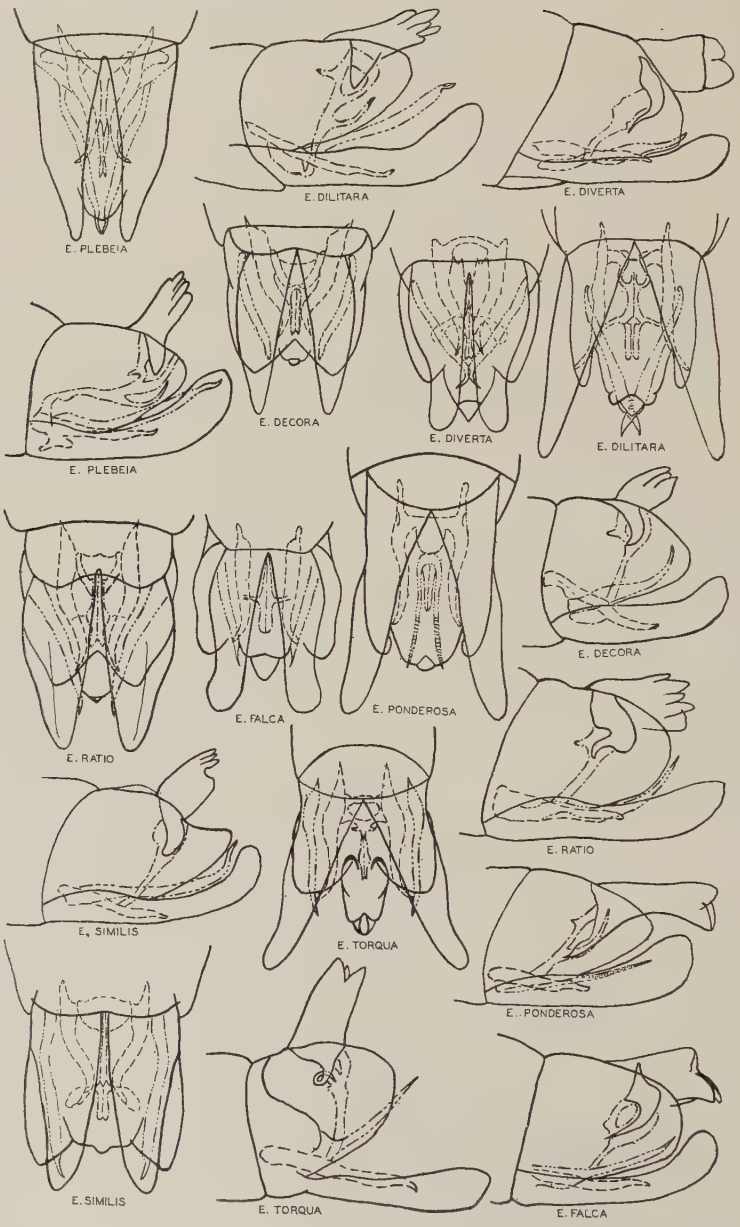
A small pale species with markings as in *aspersa*. Length, 2.5–3 mm.

Vertex bluntly rounded, almost twice as wide between eyes as length at middle.

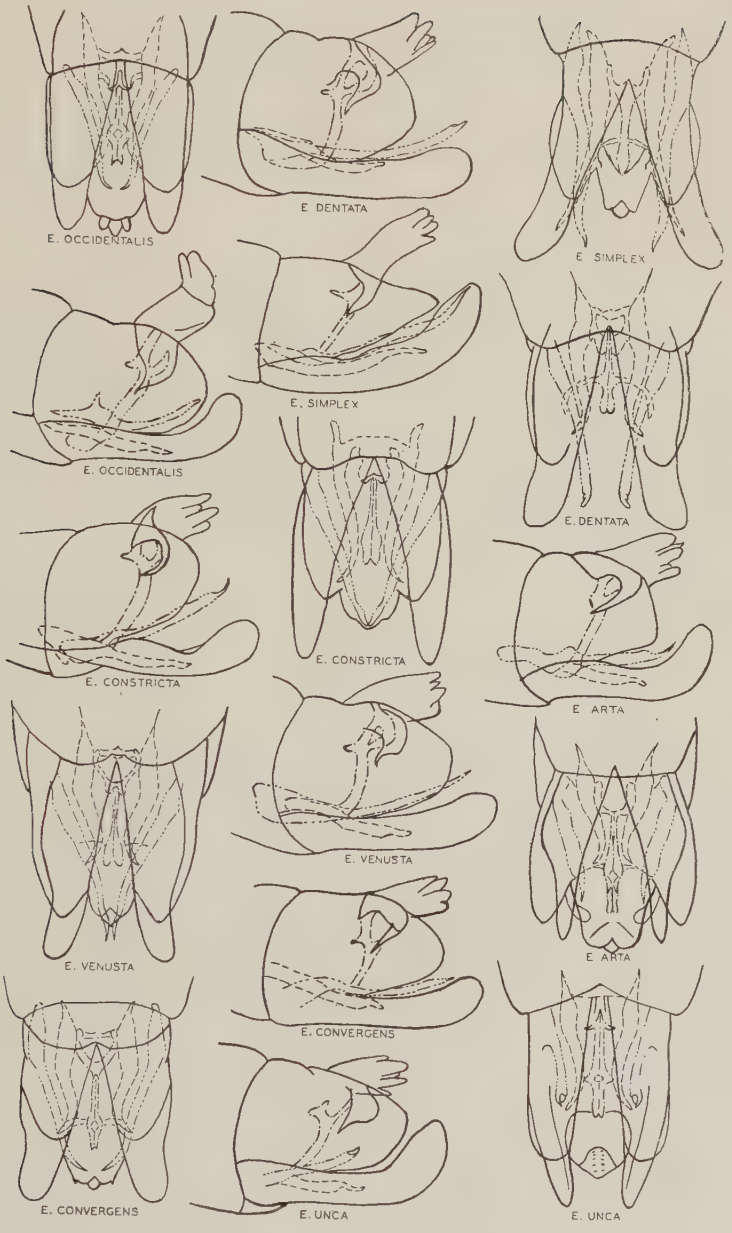
Color.—Milky white to pale green. Vertex, pronotum, and scutellum sparsely stippled with small dark dots. Wings mottled with dark pigment as in *aspersa*.

Genitalia.—Female last ventral segment broadly, roundedly produced. Male plates long, gradually tapered to sharp pointed apices and heavily set with long spines. Of the male genital pieces, the lateral processes of the pygofers in ventral view appear broad near apex where they are narrowed on inner margin and form slender finger processes which curve inwardly. In lateral view they curve abruptly dorsally near apex with apical tip curved slightly caudally. Dorsal spine short and broad, directed ventrally and curved slightly anteriorly.

Described from five male specimens from Carson City, Nevada, collected August 9, 1929, by R. H. Beamer. Male holotype in Kansas University collection.



Ventral and lateral views of male genitalia showing styles, lateral processes, dorsal spine and oedagus in normal position in the genital chambers.



Ventral and lateral views of male genitalia showing styles, lateral processes, dorsal spine and oedagus in normal position in the genital chambers.

THE EMBRYOLOGY OF THE WHITEFISH *COREGONUS CLUPEAFORMIS*, (MITCHILL)[1]

Part III.

The Second Half of the Incubation Period

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As pointed out in the second paper of this series, it is during the first half of its normal incubation period that the embryo of *Coregonus* undergoes a differentiation of its primitive embryonic tissue into definitive organs. This differentiation applies to every organ system. It remains for the second half of the incubation period to develop these structures to such a state as to produce a self-supporting, highly co-ordinated individual organism at the time of hatching. Thus it is to be expected that the major changes which occur during this latter period involve chiefly such processes as growth, change in proportion of parts, and further differentiation of tissues.

Stage 608. O. S. U. Series.—(Incubation period, 102 days, 4 hours; 191 T. U. Total length of embryo, 10 mm.; 64 pairs of somites. Reconstruction drawings, Plate V., Figs. A. B. C.)

The embryo has continued its growth in size and length since the stage last described, and now has acquired a distinct fish-like appearance within the egg shell. It lies prominently above the constantly diminishing yolk sac, to which it is still broadly attached in the middle of the body. Anterior to this attachment, the head is flexed downward to conform to the curvature of the yolk. The body of the embryo, however, is sharply bent, usually in the form of a flat dextral coil on the yolk surface. The tail completes the circle and in many cases extends just past the head, beginning a second loop. This sharp torsion and flexion of the body make it impossible, as in Stage 400, to reconstruct more than the anterior portion of the embryo. The drawings of this stage are drawn at the same magnification as previous stages, and therefore permit comparative studies.

The brain is shown in Fig. C of Plate V, with the sense organs removed. The precocious development of the nervous system that has been apparent since the closure of the blastopore is possibly even more clearly shown here. The brain at this stage appears to be roughly twice its former size. This may be seen by comparing Stages 400 and 608 of Plate VI, where corresponding points on the two drawings are

[1]Parts I and II published in Ohio Journal of Science, Vol. XXXIV, Nos. 5 and 6, 1934.

connected by lines. In the latter stage is seen a great overarching of the brain, due to the expansion of the midbrain, which now overshadows all other parts in size. The optic lobes have enlarged and have grown upward, backward, and outward until laterally they greatly overhang the infundibulum. The infundibulum retains its formerly described position ventral to the midbrain, but whereas it formerly extended to well beneath the myelencephalon, its tip now barely reaches past the middle of the metencephalon. This apparent shift in position may be due to the great growth of the dorsal portions of the brain. The infundibulum itself has increased in length, and at its posterior tip is divided into a dorsal and ventral portion. The cerebellum is now a prominent transverse plate on the posterior face of the midbrain. It is confluent at its base with the midbrain in front and the walls of the medulla behind. It is flexed backward upon the latter, its backward movement being due to the expansion of the midbrain. The drawing, Fig. A, Plate V, through the median axis of the head shows that the cerebellum also penetrates the cavity of the optic lobes to a slight extent. The floor of the myelencephalon is arched through the center (Fig. B, Plate V). Laterally and immediately behind the cerebellum, its outer walls are scarcely raised above the floor. Behind this point, however, the walls rise rapidly into lateral ridges which bend toward the center and draw the fourth ventricle into a triangular cavity which rapidly diminishes to a minute canal which continues down the length of the nerve cord as the neurocoele. The forebrain at this stage bears a transverse suture which divides it into the telencephalon and diencephalon.

The anterior end of the notochord in Stage 608 (Figs. A and C) is somewhat in advance of its position in Stage 400. In the earlier stage, the notochord ended at a level somewhat behind the middle of the otic capsule. Now it extends slightly beyond the anterior margin of this capsule. This changed relationship probably is brought about through the growth and backward crowding of the brain and its sense organs, rather than any forward growth of the anterior end of the notochord, which is to be regarded as a relatively fixed point. The changes described above also have resulted in bringing the tip of the infundibulum and the anterior end of the notochord into close proximity, a relation which persists for the remainder of the embryo's development.

The prominent lateral branchial folds ventral to the otic capsule are in the same relative position as seen in Stage 400. However, the anterior end of the pharynx now extends much farther forward than previously described. Apparently a marked forward growth of the anterior end of the pharynx has occurred (see Plate VI). The upper and lower sheets of epithelium which line the primitive mouth cavity now run forward beneath the infundibulum from the level of the branchial folds to the level of the optic nerve. Here the epithelium is in contact with the superficial layer. Between the oral epithelium above and the floor of the brain lies a sheet of cartilage, which forms the base of the chondrocranium.

The three sense organs, namely, the nasal pit, the eye, and the otic vesicle, have undergone enlargement and marked development

since being last described (Fig. B, Stage 608). The nasal pit is deeper, larger and more terminal. The eye, by comparison, is considerably larger and somewhat rotated in position. The semicircular canals of the otic capsules have continued their development and now occupy a large portion of the space within the inner ear.

The roots of the olfactory, optic and trigeminus nerves were traceable in earlier stages and were plotted on the reconstruction drawings of them. Now they are larger and more clearly defined. In addition, it is possible to plot the placodes of cranial nerve III, and a placode composed of components of cranial nerves IX and X.

Stage 784. O. S. U. Series.—(Incubation period, 131 days, 12 hours; 324.5 T. U. Total length of embryo, 12 mm.; 64 pairs of somites. Reconstruction drawings, Figs A_1, B_1, C_1, of Plate V.)

Hatching occurred in this series of embryos at stage number 803, at a total of 355 thermal units of incubation. The present stage is therefore within a few days of hatching, and for purposes of this study can be regarded as equivalent to that stage. Mrs. Fish (1929) has described a specimen of the Whitefish at the time of hatching, and gives its total length as 12 mm., the same as recorded above for embryos at this stage. The actual length of the incubation period of the Whitefish probably depends upon a variety of both extrinsic and intrinsic factors which have yet to be studied experimentally for this species.

At the stage listed above, or just before hatching, the yolk sac is reduced to a vestige of its former size and it is more narrowly attached to the embryo than in earlier stages. The embryo itself is tightly coiled, with its tail passing around the head to describe one and one-half circles. The head and body have undergone changes in proportion which give it the appearance of the newly hatched fish. The eye is prominent and heavily pigmented with stellate chromatophores on a golden ground color. The pectoral fins are well developed and active in their "fluttering" movements, although they lack the definitive pterygiophores of the adult. The median fin fold is continuous from the dorsal to the ventral median line around the tail. The tail is active, and the movements of the embryo within its shell are conspicuous in living material.

Figures A_1, B_1 and C_1, of Plate V, represent reconstruction drawings of the head of such an embryo, drawn in the sagittal plane and from the surface view, with and without the sense organs. By comparison of the second figure, Fig. B_1, with the corresponding one of Stage 608, Plate V (also Plate VI), it is seen that in the interval between these two stages, there has been a marked prolongation of the anterior portion of the head into a snout, a change which has greatly modified the contour of the head and which has been accompanied by important changes in the relative positions of the neighboring parts. For instance, the telencephalon has grown in size and has become projected into the snout. It has carried with it the nasal pit, which was thereby shifted from a position subventral on the head to one that is terminal. The epiphysis has arisen as a conspicuous outgrowth from the roof of the diencephalon. The meso-diencephalic fold, which was so prominent in Stage 608, is less conspicuous laterally and at this stage is to be seen

only in the median line. Internally, Fig. A_1, the diencephalon is more clearly delimited from the adjacent portions of the brain. The velum transversum and the meso-diencephalic fold appear as distinct ingrowths from the dorsal wall in the median line and indicate the anterior and posterior limits of the roof of the diencephalon. Below, the recessus opticus and the tuberculum posterius serve as corresponding landmarks. The major change that has occurred in this region is the very marked thickening in the floor, lateral walls and roof of the infundibulum. These form the thalami and optic chiasma. The large fiber tracts within them are now clearly differentiated. This thickening of the infundibular walls has greatly reduced the size of the diocoele and compressed it laterally until it remains little more than a vertical slit. The dorsal, anterior, median wall of the infundibulum continues uninterruptedly into the greatly thickened floor of the midbrain which constitutes the crura cerebri. The mesencephalon has undergone a process of general enlargement, brought about by a thickening in its walls. The direction of growth has largely been lateral, in such a way that this portion of the brain now greatly overhangs the infundibulum and overarches the eyes. The thickened walls have developed at the expense of the mesocoele, compressing it laterally to reduce it to a relatively narrow ventricle. The metencephalon likewise has grown laterally to an extent equal to that of the mesencephalon, and appears externally as a transverse plate. Internally, however, the forward wall of the cerebellum is expanded to form two large lobe-shaped masses, the "valvuli cerebelli" (Herrick, 1924), typical of Teleosts. These valvuli project into the cavity of the midbrain, completely filling it in its posterior portion. Since the greater bulk of these valvuli is lateral to the midline, it is not shown on the drawing of the median section.

The nasal pit and the eye are completely differentiated as described above. The semi-circular canals can be seen as of typical adult structure. At their apices they bear ampullae lined with cilia whose beating motion can readily be seen in the newly hatched larva. It is possible to locate and follow to a limited extent the course of several cranial nerves, although no special staining methods were employed in the preparation of the sections of this stage. Cranial nerves I, II, and III appear essentially as described in previous stages. The trochlearis (NIV.) arises from the lateral wall of the cerebellum as a very small nerve, which cannot be traced in this material beyond its base. The large prootic ganglion which was interpreted in Stage 608 as being composed of cranial nerves V and VII remains as a single mass. A single ganglion with two principal roots which emerge in close proximity to the inner surface of the ear is interpreted as being composed of components of the cranial nerves IX and X. The writer has been unable to identify a separate auditory nerve. An unidentified ganglionic mass lies ventral to the ear.

From the foregoing descriptions it is very apparent that before *C. clupeaformis* hatches, it possesses well differentiated sense organs. They are developed far in advance of corresponding organs in *Serranus* and in certain other species.

Several significant changes have occurred in the bucco-pharyngeal

region. It will be recalled that in Stage 608, the foregut had begun its migration forward from its primitive position and at that stage it had progressed to the level of the optic nerve. Since that stage, with the development of the snout, this forward migration of the anterior end of the pharynx has continued, being carried forward with the anterior end of the head. The mouth opening has broken through terminally in its adult position. The bucco-pharyngeal cavity is lined with an epithelium which is laden with spherical, glandular taste buds, irregularly distributed. These resemble the taste buds of the Carp, as described by Edwards (1930), and probably are similar histogenetically. The sides of the pharynx are now perforated by five pairs of fully developed visceral clefts, separated by four pairs of visceral arches. In each arch can be traced the supporting strand of cartilage which bears a ridge of primary gill filament. The secondary, finger-like gill filaments do not form on these primary gill filaments until after hatching. This failure of the secondary gill filaments to develop before hatching may be widespread in the teleosts. The author (1931) has found a similar condition in *Micropterus dolomieu*, where the secondary filaments are first developed a few days after hatching. M. Plehn (1901) describes their differentiation in the perch apparently from larval material. An aortic arch extends through each gill arch at the base of the filament, and the circulation of blood through these vessels can be clearly observed in living material. The heart has considerably increased in size since stage 608, and the ventral aorta running forward from it enters the floor of the pharynx at the point of attachment of the first anterior gill arch. In the previous stage, it disappeared in the floor of the pharynx at a point correspondingly much more posterior.

The branchial cartilages are attached ventrally to the median hyoid cartilage and dorsally to the cartilage in the floor of the chondrocranium, both of which are developed at this stage. The base of the chondrocranium extends as a sheet beneath the brain for the entire length of the head forward from the anterior end of the notochord. The lower jaw is supported by Meckel's cartilage. To its posterior angle is attached the base of a rudimentary operculum. At the time of hatching, the operculum extends backward to cover the first two pairs of gill arches.

Posterior to the region shown in the reconstruction drawings, a relatively advanced state of differentiation has been attained by the various organs. The pectoral fins and median fin fold are described above. Body, tail, and pectoral fin movements are strong and vigorous for some time before hatching. The body wall muscles have well differentiated striated myofibrils. The pronephric ducts can be traced backward throughout the length of the body. They converge in the median line caudally and fuse into a single tube in the region of the anus. The blood vessels throughout the body are well differentiated. They are lined by a distinct endothelium and many are congested with blood cells. Such vessels as the internal carotid artery, jugular vein, hepatic portal vein, duct of Cuvier, the aortic trunks and dorsal aorta fall in this category. In living, newly hatched larva, the circulation of the blood in the main vessels can be clearly traced throughout the body.

DISCUSSION

It is clearly evident from the description of the later stages of embryonic development of the Whitefish that this species attains a high degree of differentiation in its tissues previous to hatching. As pointed out earlier in this paper, the anlagen of all of the major organ systems are clearly established during the first half of the greatly prolonged period of incubation. This condition leaves the embryo free to undergo extensive development and differentiation of these tissues for the remainder of its incubation period. Since the eggs are normally laid during the months of November and December, and do not hatch until the first few days of April, the period of incubation in point of time is comparatively long. In the present series, the incubation period lasted 134 days, at winter lake temperatures, slightly above freezing (1.5° C.). This is equivalent in thermal units to an incubation period of almost nine days at a temperature of 22° centigrade. In comparison with species whose eggs normally are developed under this higher temperature, in the late spring or in the laboratory, the Whitefish has a relatively long period of incubation. Such a period then may be regarded as permitting a high degree of differentiation to occur. These two factors of length of incubation period and the degree of differentiation attained by the embryo before hatching are undoubtedly closely co-ordinated.

The whitefish is typically teleostean in its embryology. The cleavage pattern of the egg and its mode of early development compares very closely with the classical descriptions of Wilson for *Serranus*, of Klein and Henneguy for the trout, of Kuntz and others for other teleosts. The process concerned with gastrulation and closure of the blastopore, and the subsequent organogenesis is in general consistent with such processes in other teleostean species, so well summarized by Brachet. However, a review of the three papers in this study will reveal several outstanding features in which *Coregonus* is distinct in its embryological development.

The astral systems are unusually conspicuous in the mitotic figures of the segmenting blastomeres in the early cleavage stages. The astral rays extend from the centrosphere in all directions to the periphery of the cell. Those rays which radiate from opposite centrosomes cross each other in the center

of the mitotic figure. They are not obscured in this region by the chromosomes, since the latter are extremely minute.

The anlagen of all the organ systems are definitely established in the first half of the incubation period. By the end of that period, Stage 400, O. S. U. Series, all the definitive parts of the adult brain are present as such. The eye is fully formed. The nasal and auditory pits have already sunken in from the surface ectoderm and have established a nervous connection with the brain. The heart and the chief definitive vessels contain blood cells and circulation has become established. The pharyngeal pouches are well developed, and the gut is closed over for most of its length and possesses a lumen. The liver is present. The notochord is fully vacuolated, and the adult number of paired muscle somites is present. Even the anlagen of the paired lateral fins are distinct. The embryo has attained two-thirds of its hatching length. In short, all the significant phases in the development of these various structures occur during the first half of the incubation period.

The whitefish serves admirably for the study of certain embryological features peculiar to teleosts. The process of the proliferation of erythrocytes from the intermediate cell mass in the median line of the embryo's body can be clearly traced. Again, the brain is precocious in its development. By the hatching stage, the relatively large size of the optic lobes, infundibulum, and the thalamus indicate an unusual degree of development in these regions.

The valvuli cerebelli, the gills, and fins are all well-known characters peculiar to teleosts. But it is of some interest to observe that these are among the last structures in the whitefish embryo to become differentiated, a fact which points to their specialized character. The swim bladder does not develop until after the hatching stage.

The whitefish undergoes a very radical shift in the position of its mouth during the latter half of the embryonic period. The primary ventral position of the forward end of the pharynx in close apposition to the infundibulum is unquestionably primitive and is suggestive of the ventral mouth of more primitive fishes. The migration forward of the anterior end of the pharynx to bring the mouth opening to the tip of the head is a conspicuous feature of whitefish development.

SUMMARY

This paper is the result of a preliminary study of the embryology of the whitefish, *C. clupeaformis*, of the Great Lakes, from fertilization to hatching. It is based upon a series of 803 egg stages. The eggs were taken at four hour intervals, day and night, throughout the period of incubation, a total of 134 days and 16 hours. In this series, those stages involving early cleavage, germ ring formation, the primitive streak, the formation and closure of the blastopore, and the differentiation of the primary germ layers are described in Paper I. Organogenesis from this point to hatching is discussed in Papers II and III, accompanied by reconstruction drawings. These trace the general development of the brain, sense organs, cranial nerves, notochord, muscle somites, pronephric tubules, the gut, branchial folds, and the heart.

The whitefish is in general typical of the teleosts in its major embryological processes. Its extended period of incubation makes it favorable embryological material, because of the possibility of obtaining closely graded series of embryonic stages. Outstanding features in the embryology of this series include (1) conspicuous astral systems in the segmenting blastomeres, (2) precocious differentiation of organs during the first half of the incubation period, (3) the marked forward migration of the mouth from a ventral to a terminal position, and (4) the relatively high degree of differentiation of the brain, gills and other organs just previous to hatching.

TABLE I

SYNOPSIS OF THE EMBRYOLOGY OF THE WHITEFISH, *Coregonus clupeaformis*

Stage No. O. S. U.	Age in Days	Age in Thermal Units	Total Length, mm.	No. of Somites	Description
1	1	8	.....	.....	8-celled blastodisc.
8	2	15	.....	.....	Blastodisc 4 cells deep. Epidermic stratum forming. Early periblastic ridge.
16	3½	30	.....	.....	Blastodisc 8-10 cells deep. Blastomeres reduced in size.
32	6	42	.....	.....	Formation of germ ring and subgerminal cavity. Syncytium of scattered nuclei in central periblast.
48	8	60	.....	.....	Germ ring is migrating around yolk. Blastoderm envelops upper one-third of yolk. Embryonic bud and primitive entoderm appear.

TABLE I—Continued

Stage No. O. S. U.	Age in Days	Age in Thermal Units	Total Length, mm.	No. of Somites	Description
64	11	82	.....	.....	Germ ring lies in equatorial plane. Embryonic shield forming. Ectodermal layer differentiated beneath epidermic stratum. Notochordal area outlined. First step in formation of the neurenteric streak.
80	14	93	.....	.....	Primary germ layers are established. Blastoderm encloses two-thirds of yolk.
96	16	97	2.0	.....	Large yolk plug stage. Formation of primitive streak. Kupffer's vesicle appears. Lateral mesodermal plates distinct from surrounding layers. Neural keel forming in anterior end.
112	19	103	2.32	3 prs.	Optic primordia appear as solid cell masses. Narrow yolk plug stage.
128	22	108	2.96	11 prs.	Closure of blastopore. Three primary cerebral vesicles have developed. Solid neural keel. Notochord extends forward to level of midbrain. Kupffer's vesicle has reached its maximum development. Sensory plate appears laterally on the head.
144	24	112.5	.....	14 prs.	Embryo extends one-half distance around curvature of the yolk, without torsion. Small cavities within optic sacs and forebrain. Auditory pit anlagen. Conspicuous but incomplete branchial folds. Incipient stages in formation of pericardial cavities.
160	27	115	3.5	21 prs.	Increased size of brain and optic vesicles. The latter are invaginated to form a two-layered optic cup, with choroid fissure and primordium of lens. Nasal pit anlagen appear. Single endocardial mass beneath pharynx, in midline. Incipient stage in formation of pronephric chamber and duct.
176	30	117.8	.....	24 prs.	Progressive development of features listed above.
192	32	120	.....	28 prs.	Midbrain divided into two distinct optic lobes, hindbrain into meten- and myelencephalon. Fourth ventricle formed. Optic stalk. Tail is distinctly raised above yolk, and is undercut by tail fold.
208	35	123	.....	32 prs.	Forebrain differentiated into telen- and diencephalon. Infundibulum in initial stages of development. Hyomandibular and first branchial pouches in contact with surface ectoderm. Small lumen in gut.

TABLE I—Continued

Stage No. O. S. U.	Age in Days	Age in Thermal Units	Total Length, mm.	No. of Somites	Description
224	38	126	4.2	39 prs.	Nasal pit is elliptical, lined with columnar epithelium. Increased size of brain and eye is conspicuous. Prominent 4th ventricle. Vacuolation of cells of notochord is evident throughout its length. First anterior branchial pouch has broken through to form an open gill cleft. The second branchial pouch is formed. Gut is closed throughout its length. Position of future anus appears at level of 36th–37th somites. Paired dorsal aortae appear. Heart progressively developed. Pronephric chamber possesses a distinct cavity. Its duct extends to anal region. Continuous fin fold around tail.
272	46	134	.....	49 prs.	Liver appears, as ventral outgrowth from midgut, at level of sixth somite.
288	48	136.4	.....	52 prs.	The 3rd and 4th branchial pouches appear. Myofibrils have formed in somites throughout middle of trunk. Embryonic coelom is conspicuous at this level.
304	51	139	.....	56 prs.	Pectoral fins appear.
320	54	142	.....	62 prs.	Notochord surrounded by hyaline sheath. The dorsal aorta is traceable into tail region. Caudal vein and subintestinal vein appear. Gut possesses distinct lumen throughout its length.
352	59	147	.....	62 prs.	Pronephric chambers at level of 4th and 5th somites possess glomeruli in their walls, receiving branches from the dorsal aorta.
368	62	150	.....	64 prs.	The complete hatching number of somites is attained with this stage. Cross-striations occur in myofibrils of anterior somites.
400	67	155	8	64 prs.	Embryo forms an almost complete circle on yolk. Brain lobes have become greatly expanded laterally. Columnar epithelium is well differentiated in gastric region of gut. The heart is looped in the form of a U-tube and is suspended by mesocardium. Vitelline veins are large and filled with erythrocytes. Auditory vesicle irregular in outline, with ampullae and semi-circular canals developing within. Pectoral fins definitely raised above surface of lateral somatopleure. The preauditory sensory placode is evident, lying on the side of the head, anterior to hyomandibular pouch.

TABLE I—Continued

Stage No. O. S. U.	Age in Days	Age in Thermal Units	Total Length, mm.	No. of Somites	Description
608	102	191	10	64 prs.	Embryo forms a complete circle on yolk, with tail extending past the head, beginning a second loop. It has a distinct fish-like appearance. Yolk sac diminishing in size. This stage is marked by a great enlargement of the brain lobes, and a shift in their relative position. The posterior tip of infundibulum is divided into a dorsal and ventral portion. The anterior end of the pharynx has migrated forward beneath the infundibulum to the level of the optic nerve. Semicircular canals of inner ear are distinct. Roots of cranial nerves I, II, III, V, VII, IX, and X are plotted on reconstruction drawings.
784	131	324.5	12	64 prs.	Embryo forms 1½ circles on yolk. Approximately hatching condition. Yolk sac reduced to a vestige of former size. Eye heavily pigmented with stellate chromatophores. Active movements of pectoral fins, tail and tail fin in living material. Prolongation of head into a snout, with corresponding changes in forward portion of brain. Fiber tracts are differentiated within the thalamus and optic chiasma. Valvuli cerebelli project into cavity of midbrain. Progressive development of sense organs and cranial nerve roots. Mouth cavity has broken through in its adult terminal position on the head. Taste buds line the mouth cavity. Four pairs of gill arches are open on sides of head, partly covered by operculum. Primary gill filaments present. Meckel's cartilage and the base of the chondrocranium are differentiated. The principal definitive blood vessels are traceable throughout the body.
803	134	355	12	64 prs.	Hatching stage.

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EXPLANATION OF PLATES

Plate V

Reconstruction drawings of Stages 608 and 784, O. S. U. Series, anterior end of embryo.

Figs. A and A_1—Median sagittal sections of the head in Stages 608 and 784, respectively.

Figs. B and B_1—Lateral view of head, in Stages 608 and 784, respectively, showing sense organs.

Figs. C and C_1—Surface of brain, without sense organs, in Stages 608 and 784, respectively, showing bases of cranial nerves, branchial arches, etc.

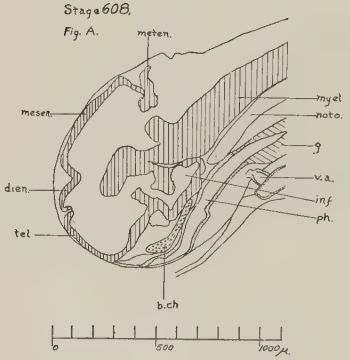
Plate VI

Reconstruction drawings of Stages 224, 400, 608, and 784, with the corresponding areas or points connected by lines, to show the changes in proportion and relationships during development. The base line is drawn through the center of the auditory vesicle.

(All figures are drawn at the same magnification.)

ABBREVIATIONS USED IN PLATE V

aud.—auditory vesicle.
br. a. I–IV—branchial arches, 1–4.
b. ch.—basis cranii.
cr. c.—crura cerebri (caudal peduncle).
dien.—diencephalon.
ep.—epiphysis.
g.—gut.
g. m.—ganglionic mass.
ht.—heart.
inf.—infundibulum.
m. d. f.—meso-diencephalic fold.
Meck.—Meckel's cartilage.
mesen.—mesencephalon.
meten.—metencephalon.
myel.—myelencephalon.
n. I, II, etc.—cranial nerves.
nas.—nasal pit.
noto.—notochord.
op. ch.—optic chiasma.
ph.—pharynx.
r. o.—recessus opticus.
t. p.—tuberculum posterius.
tel.—telencephalon.
th.—thalamus.
v. IV—fourth ventricle.
v. a.—ventral aorta.
v. c.—valvuli cerebelli.
v. t.—velum transversum.


Stage 608.
Fig. A.
meten.
mesen.
myel
noto.
dien.
tel
v.a.
inf.
ph.
b.ch
0
500
1000 μ.

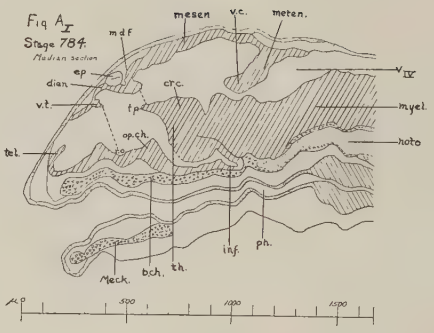


Fig A I
Stage 784
Median section
mesen
v.c.
meten.
m d f
ep
dien.
v.t.
c r c.
t p
op.ch.
tel.
myel.
noto
inf.
ph.
Meck.
b.ch.
th.
μ
500
1000
1500

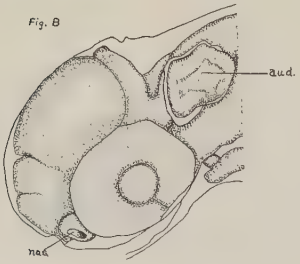


Fig. B
aud.
nas.

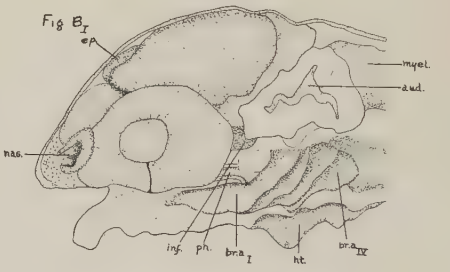


Fig B I
ep
myel.
aud.
nas.
inf.
ph.
br.a I
ht.
br.a IV

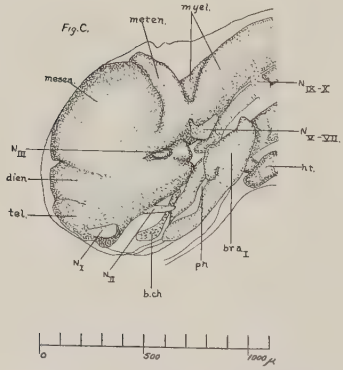


Fig. C.
myel.
meten.
mesen.
N IX-X
N V-VII
N III
dien.
tel.
ht.
N I
N II
b.ch
ph
br.a I
0
500
1000 μ

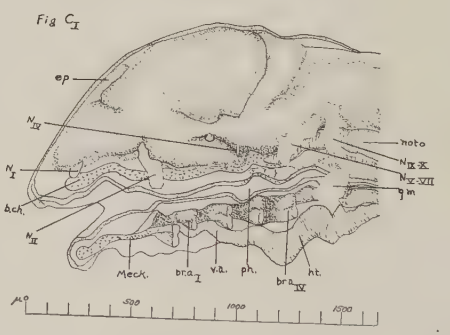
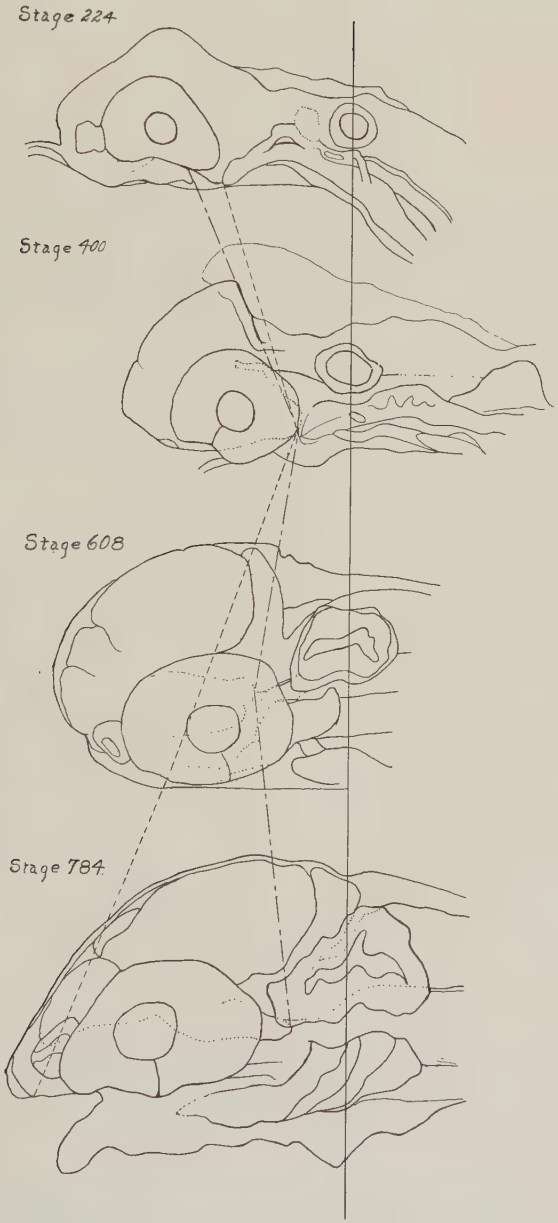


Fig C I
ep
N IV
noto
N IX X
N V-VII
g m
N I
b.ch
N II
Meck.
br.a I
v.a.
ph.
br.a IV
ht.
μ
500
1000
1500


Stage 224
Stage 400
Stage 608
Stage 784

THE ALIMENTARY CANAL OF CALASOMA SYCOPHANTA LINNEAUS

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In the following discussion are presented the results of investigations made upon the general morphology and histology of the digestive tract of the carabid beetle *Calasoma sycophanta* Linnaeus. These studies were made principally upon hibernating beetles.

This beautiful green metallic beetle is a native of Europe but has become abundant in New England since its introduction in 1906 to aid in the control of the gipsy moth (*Porthetria dispar* L.).

METHODS

The material was collected at various points in New England during the early summer of 1932 and 1933. The bulk of the material was kept alive in moist sphagnum moss until ready to make the dissections for laboratory study.

Beetles were taken from the hibernation container and dissected in normal saline solution for general anatomical studies. Where the tract was to be used for histological studies the specimen was first killed in a cyanide bottle and then dissected in Kahle's solution. The alcohols and Cedar Oil were used for dehydration and clearing. Difficulties were encountered in staining the sections. One stain might be fairly good for one region of the tract while it would not take at all in another region. Delafield's Haematoxylin and Eosin, as well as Heidenhain's Iron-Haematoxylin, gave only fair results in the posterior portion of the tract.

In making drawings, either a Camera Lucida or a projection machine was used for making the outlines and putting in as many of the cell walls and nuclei as stood out vividly. The minute details were put in free hand by the aid of a planescopic

[1]The writer is indebted to Dr. C. H. Kennedy for his helpful suggestions and criticisms of this work, also to Mr. C. W. Collins, and his entomological assistants at the Gipsy Moth Laboratory, for assistance in obtaining material for these studies.

microscope. All drawings might be classed as diagramatic but care was taken to present the material as much like the actual sections as possible.

GROSS ANATOMY OF THE DIGESTIVE TRACT

GENERAL ANATOMY

The alimentary canal in this carnivorous species is only slightly greater in length than the insect's body. The three primary divisions of the canal, based on embryonic origin, are distinct and their limits are well marked. The relation of these primary divisions (stomodaeum, mesenteron, and proctodaeum) to each other, and their component parts, is shown in Fig. 1, Plate I.

FORE-INTESTINE

The fore-intestine (stomodaeum) is little more than an elongated thin-walled sac, except for the gizzard which lies just anterior to the oesophageal valve. The fore-gut extends caudad into the mesothorax, comprising slightly less than one-third of the total length of the entire canal.

The pharynx is the slightly dilated portion of the fore-gut just posterior to the mouth, which connects the mouth with the oesophagus.

The oesophagus is nothing more than a simple tube of variable length connecting the pharynx with the crop. It lies in the posterior portion of the head and the anterior one-third of the prothorax. The only essential difference between this region and the two it connects is size, the oesophagus being the smallest. Apparently the pharynx and oesophagus have no function other than that of conduction.

The crop is present as a dilation of the tract immediately posterior to the oesophagus. It is a rather capacious thin-walled sac lying in the posterior two-thirds of the prothorax and the anterior portion of the mesothorax. In all the freshly killed specimens dissected the crop contained enough air to keep the walls distended although little food was present in the digestive tract of these hibernating individuals.

The gizzard is a thick-walled oval region lying just posterior to the crop and bounded posteriorly by the oesophageal valve. This portion of the tract lies within the mesothoracic segment. It is generally referred to as a grinding organ.

The oesophageal valve shows up externally as a distinct constriction of the tract immediately posterior to the gizzard, marking the division between the fore- and mid-intestines. This structure is located near the junction between the mesothoracic and metathoracic segments. It possibly functions in preventing regurgitation.

MID-INTESTINE

The mid-intestine (mesenteron) or stomach forms a conspicuous part of the alimentary canal, although comprising only about one-third the total length of the tract. It is bounded anteriorly by the oesophageal valve, located near the anterior part of the metathorax, and posteriorly by the pyloric valve and Malpighian tubules, located in the fourth

abdominal segment. There is a gradual reduction in the diameter of the mid-intestine from about the middle toward the posterior end at the pyloric valve. The stomach is a slightly tortuous tube, invested with numerous closely packed small villus-like enteric coeca, but the latter are much reduced on the posterior third. The coeca vary in size and shape as to whether beetles are in a hibernating or active condition. In the hibernating forms the crypts are small and finger-like in shape, while the crypts of actively feeding individuals are larger and bulbous at their bases. It is in the region of the stomach that most of the secretion (and absorption?) takes place.

HIND-INTESTINE

The hind-intestine (proctodaeum) comprises slightly more than one-third the total length of the tract and is differentiated into three regions.

The pyloric valve is located at the union of the mid-gut with the hind-gut, where the Malpighian tubules arise. This valve supposedly serves to close the posterior end of the stomach.

The Malpighian tubules are attached in the region of the pyloric valve and are four in number. All arise separately and at about equal distances apart around the tract. The bulk of the excretory tubules lies within the general region of the pyloric valve, but they extend as far anteriorly as the metathorax, and as far posteriorly as the sixth abdominal segment. The total length of the four tubules is approximately sixty centimeters. Many beetles were dissected and in no case were there loose ends of Malpighian tubules found. Evidently they unite distally but the four do not always make a common union, if ever. The diagram in Fig. 7, Plate II, shows a fusion of tubules found in one dissection, but no duplication of this in other individuals was found. Frequently two tubules are found which are superficially fused, but by careful dissection they can be separated.

The ileum, frequently called the small intestine, is not easily differentiated from the colon in gross dissection. It follows a rather irregular course but lies almost wholly within the fourth abdominal segment. Its function is obscure.

The colon links the distal end of the ileum with the proximal end of the rectum. It is a rather tortuous tube confined almost entirely to the fifth abdominal segment. At the posterior end, where it unites with the rectum, it is considerably reduced in size. Functionally the colon is a conduction tube.

The rectum is quite large and lies within the fifth and sixth abdominal segments. Six rectal pads are visible along the anterior portion of the rectum. The rectum connects the colon with the anus.

HISTOLOGY OF THE ALIMENTARY CANAL

FORE-INTESTINE

The histological structure of the fore-gut is quite uniform throughout its parts with the exception of the gizzard. An examination of the sections of the wall of the fore-gut shows the following tissues from

within outwards: (1) Intima of cuticula or chitin, (2) Epithelium of hypodermal cells, (3) Longitudinal muscles, (4) Circular muscles, and (5) "Peritoneal membrane" of connective tissue cells. In the gizzard there are, in addition to the above, spines which arise from the intima and project into the lumen.

The fore-intestine is lined throughout with a rather heavy layer of non-cellular cuticula or intima. It projects into the lumen of this portion of the tract in irregular wave-like folds. In the gizzard this layer is much heavier and thickened in such a manner that in cross-section it appears to be heavy teeth projecting into the lumen. There are large chitinous plumose spines which arise in the intima of the gizzard and project more or less caudad into the lumen. These ridges of heavy intima probably function in grinding up particles of food while the spines possibly tend to prevent the food from being forced anteriorly during the grinding process.

The epithelium which is composed of flattened irregular hypodermal cells forms the tissue just outside the intima in the oesophagus and crop. In the gizzard the epithelium is composed of rather regular cells.

In the oesophagus and crop there lies immediately outside the epithelium a series of bundles of longitudinal muscle tissue. There are usually six such bundles located at fairly regular intervals around the tract. There are associated with these bundles of longitudinal muscles small ducts which are probably trachae. In the region of the gizzard the longitudinal muscles form four large bundles, alternating with the chitinous projections of the intima, which are an important part of the crushing or grinding apparatus.

Surrounding the longitudinal muscle layer in the oesophagus and crop is a rather uniform layer, one or two strands in thickness, of circular muscle tissue. In the gizzard this layer of circular muscles is much thicker, being composed of several strands.

MIS-INTESTINE

The mid-intestine or stomach is markedly different from the fore- and hind-intestines in that there is no intima and the relative positions of the circular and longitudinal muscles are reversed.

Through histological study the following sequence in the positions of the tissues is found in the stomach from within outward: (1) Digestive epithelium of endoderm cells supported by a basement membrane, (2) Circular muscles, (3) Longitudinal muscles, and (4) Connective tissue, known as "peritoneal membrane."

There is no evidence of a peritrophic membrane.

The cells of the digestive epithelium are slightly columnar in structure but vary in size and shape. Many sections showed evidence of a striated border. The location of the regenerative tissue, or nidi cells, was not cleared up to the satisfaction of the writer. From the study of hibernating individuals it appears that probably the regenerative tissue is located within the crypts. In Fig. 5, Plate I, a diagram of a longitudinal section of a crypt is shown which has many very small cells near the tip. Rungius (12) has illustrated the structure of the

digestive epithelium of the crypts of *Dytiscus marginalis* L. It is similar to that of *Calasoma sycophanta* L. However, these digestive epithelial cells in the crypts are frequently arranged so that their apical ends point more toward the opening of the crypt into the stomach than those shown in Fig. 5, Plate I.

Whether the very delicate basement membrane is located next to the digestive layer just described, or whether it lies just outside the layer designated X in Figs. 4 and 5, Plate I, has not been determined. The structure of this X-layer has not been adequately investigated, but it stands out very vividly in sections stained with Iron-Haematoxylin. There are nuclei (labeled Y) in this layer which may be regenerative tissue, or possibly the whole layer X is regenerative in function.

The outer layer of the crypts is composed of rather large distinct cells. This Z-layer is liberally supplied with trachae. That would indicate that the X-layer may have a large component of tracheoles.

Surrounding the X-layer in the main part of the mid-gut there are two to three layers of circular muscles. This muscle tissue is rendered less conspicuous by the numerous crypts which protrude through the wall of the stomach.

Surrounding the circular muscles are isolated strands of longitudinal muscles.

HIND-INTESTINE

Histologically the hind-intestine presents from within outwards the following tissues: (1) Intima, (2) Epithelium of hypodermal cells resting on a basement membrane, (3) Circular muscles, (4) Longitudinal muscles, and (5) Connective tissue, or "peritoneum."

The Malpighian tubules are external structures of the hind-gut which arise in the region of the pyloric valve. These tubules are made up of numerous cells with large ovate nuclei. The cells have a striated border on their inner margin. Surrounding these cells is a thin layer of connective tissue.

The pyloric valve is marked externally by the origin of the Malpighian tubules. Histologically it is a folding over of the epithelium of the hind-gut into the lumen of the mid-gut. The length of the lips of the valve varies in different individuals. The hypodermal cells of the epithelium are columnar in structure as is true of the epithelial cells of the oesophageal valve. The valve is lined with an intima of chitin which extends as far forward as the point of union between the mid- and hind-intestines. There are numerous circular muscles just outside the epithelial layer, a slight distance posterior to the union, which may function in closing the valve.

The intima of the ileum, or anterior portion of the hind-gut, is quite heavy. The intima in this region has spines which may be easily overlooked due to the digestive products which accumulate around them. The epithelial layer in this region is also quite thick and makes six large folds which project into the lumen. Just outside the epithelium within these folds are strands of longitudinal muscles. The circular muscle layer is several strands in thickness just posterior to the valve.

Strands of the outer layer of longitudinal muscles appear as six bundles immediately outside the circular muscle layer. Connective tissue is evident in some sections of the ileum.

The colon has much the same histological structure as the ileum, but differs in that the intima and epithelial layer are thinner. The size of the colon is much reduced near the point of union with the rectum.

The rectum is much larger and has a much thinner wall than the other divisions of the hind-gut. There are six rectal pads located on the inner surface of the wall of the rectum near the anterior end which may be plainly distinguished due to the thickness of the rectal wall. These pads are composed of very large cells with ovoid nuclei. The pads lie between the intima and the very delicate epithelial layer. The layer of circular muscles which lies immediately outside the epithelial layer is but one to two muscle strands in thickness. The longitudinal muscles appear outside the circular muscles as six irregular bundles.

CONCLUSIONS

The alimentary canal of *Calasoma sycophanta* L. is slightly longer than the insect's body, a length which corresponds to its carnivorous habits. The three primary regions of the canal known as the stomodaeum, mesenteron, and proctodaeum are well defined, and show the following specializations:

Stomodaeum, or Fore-intestine.—Pharynx, oesophagus, crop, gizzard and oesophageal valve. It is ectodermal in origin and thus lined throughout with chitin.

Mesenteron, or Mid-intestine.—The whole region is known as stomach and is endodermal in origin, having no intima. There are evaginations of the digestive epithelium in the form of villus-like projections, termed crypts. These increase the area of the digestive epithelium enormously, and it is this layer which has to do with the secretion and absorption connected with digestion.

Proctodaeum, or Hind-intestine.—Pyloric valve, four Malpighian tubules, ileum, colon and rectum. There are six oval rectal pads on the anterior end of the rectum. The hind-gut is lined throughout with chitin, being ectodermal in origin.

The present study of the crypts has been far from sufficient enough to clear up their histology thoroughly. It is hoped that a more complete study of these structures will be possible.

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EXPLANATION OF PLATES

Plate I

Fig. 1. A dorsal view of the alimentary canal.
Fig. 2. Cross-section through oesophagus.
Fig. 3. Cross-section through gizzard.
Fig. 4. Cross-section through crypt.
Fig. 5. Longitudinal section through crypt.

Plate II

Fig. 6. Longitudinal section through oesophageal valve.
Fig. 7. Diagram of fusion of Malpighian tubules. (See text.)
Fig. 8. Longitudinal section through pyloric valve.
Fig. 9. Cross-section through anterior portion of mid-intestine.

Plate III

Fig. 10. Sketch of crypts of a hibernating beetle.
Fig. 11. Sketch of crypts of a beetle in the active feeding condition. Drawn to same scale as Fig. 10.
Fig. 12. Cross-section of anterior ileum.
Fig. 13. Highly magnified portion of a cross-section of posterior rectum. (Muscle striations are much closer together than shown in any of these figures. There should be three muscle bands in a space the length of a muscle nucleus.)
Fig. 14. A portion of a cross-section through the region of the pyloric valve, showing entrance of Malpighian tubule.
Fig. 15. Cross-section of colon.
Fig. 16. Cross-section through a rectal pad.
Fig. 17. Cross-section of Malpighian tubule near origin.
Fig. 18. Cross-section through anterior rectum, showing rectal pads.

KEY TO ABBREVIATIONS

An. Gl.—Anal gland.
An. Gl. Res.—Anal gland reservoir.
C. Mus.—Circular muscle.
Co.—Colon.
Cr.—Crypt.
D. Epi.—Digestive epithelium.
Epi.—Epithelium.
Giz.—Gizzard.
Il.—Ileum.
Int.—Intima.
L. Mus.—Longitudinal muscle.
Lu.—Lumen.
M. T.—Malpighian tubule.
M. I.—Mid-intestine.
Oes.—Oesophagus.
Oes. V.—Oesophageal valve.
Ph.—Pharynx.
Rec.—Rectum.
Rec. Pad—Rectal pad.
Sp.—Spine.
Tr.—Trachea.
X—Layer which stains very dark with iron-haematoxylin.
Y—Possibly nucleus associated with regenerative tissue.
Z—Layer of rather large cells with distinct nuclei. Not fat cells.

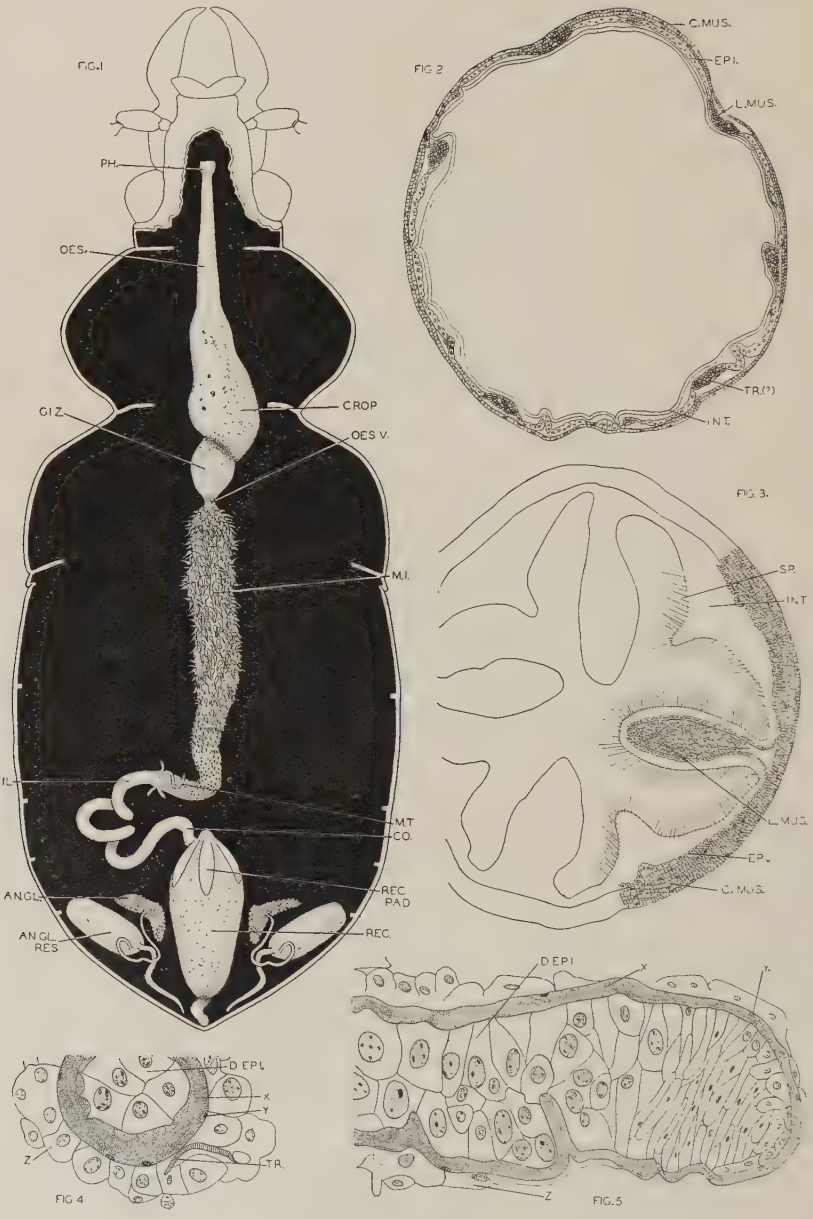


FIG.1
PH.
OES.
GIZ.
CROP
OES V.
M.I.
IL.
M.T
CO.
ANGL.
REC.
PAD
ANGL.
RES
REC.
FIG 2
C.MUS.
EPI.
L.MUS.
TR.(?)
INT.
FIG 3.
SP.
INT
L.MUS.
EP.
C.MUS.
D EPI
X
Y
Z
TR.
FIG 4
D EPI
X
Y
Z
FIG.5

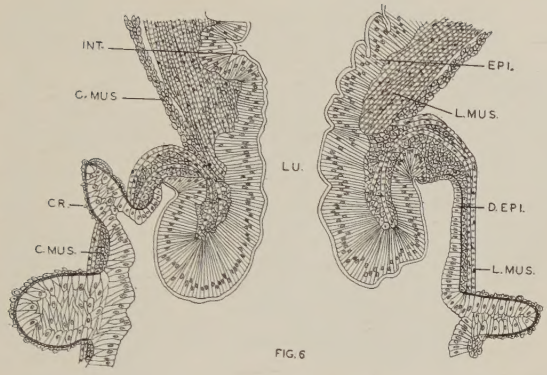


FIG. 6

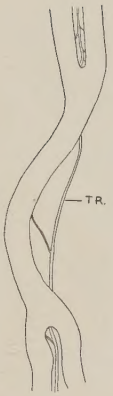


FIG. 7

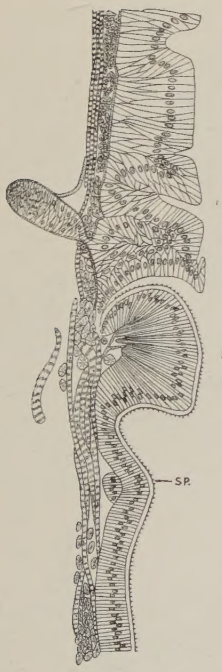
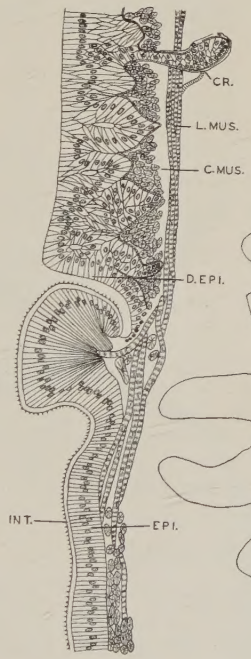


FIG. 8



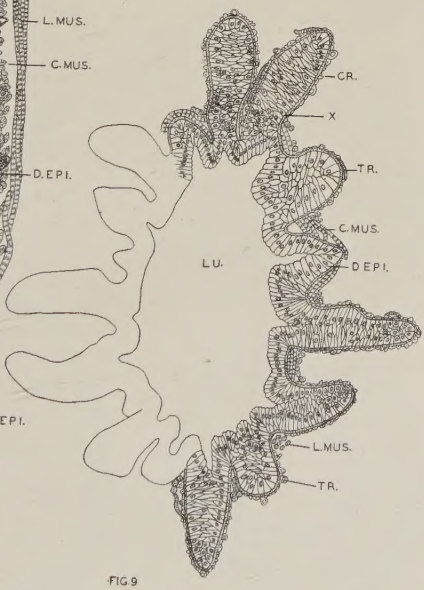


FIG. 9

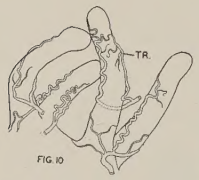


FIG. 10

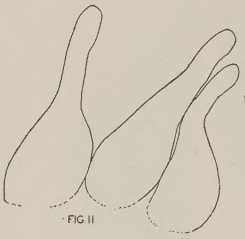


FIG. 11

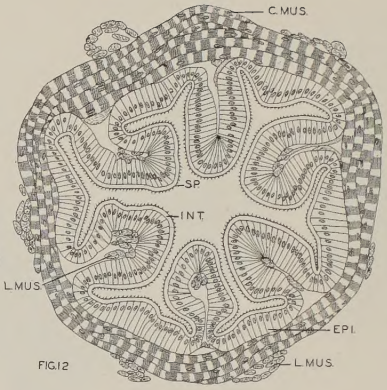


FIG. 12

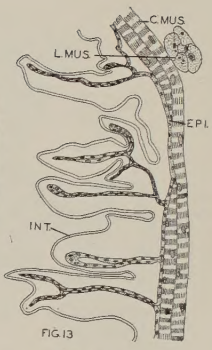


FIG. 13

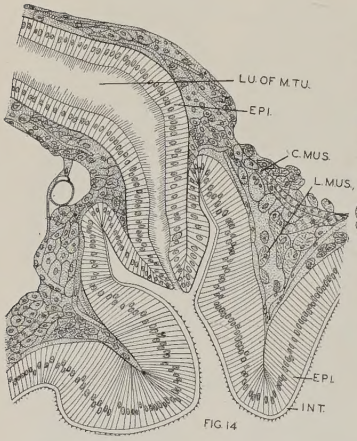


FIG. 14

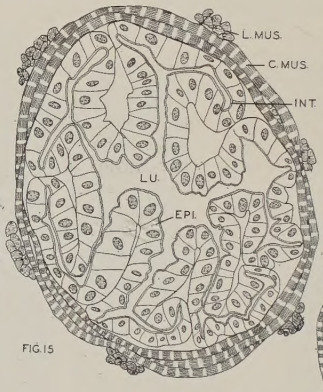


FIG. 15

FIG. 16

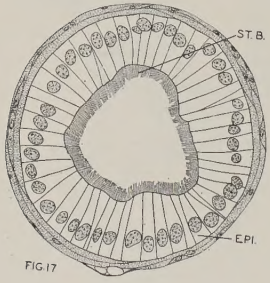


FIG. 17

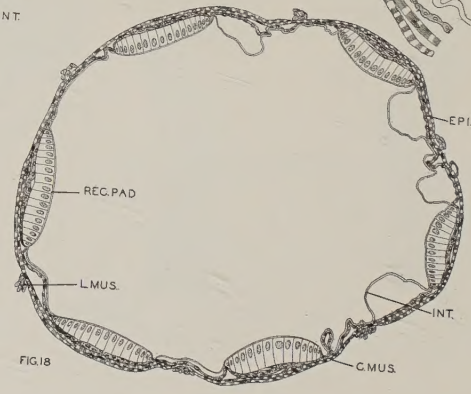


FIG. 18

BOOK NOTICES

Man and His Biological World.

This is the second part of a two-volume introductory science course, the first part of which was reviewed in the September 1934 number of this journal. The book is written in easy conversational style, and brings out in a very interesting way the basic facts of biology. The attempt to make the book interesting has, however, been somewhat overdone, resulting in a lowering of the level of prospective students. As it stands, the book should be excellent for courses in high school biology, but probably not for college students, who should by college level be ready for more advanced material than is presented in this text.—L. H. S.

Introductory Course for Science in Colleges, II, Man and the Nature of his Biological World, by F. C. Jean, E. C. Harrah, F. L. Herman and S. R. Powers. x + 589 pp. Boston, Ginn & Co., 1934.

Health and Disease

This monumental volume is written to give to medical students, clinicians and practicing physicians a fundamental understanding of the principles of physiology which underlie the workings of the human body in health and disease. It is an inclusive and all-embracing volume, covering in its nearly 1,200 pages the methods of physiology, the principles involved, and a wealth of detailed information, with appropriate citations to the literature. Inevitably some subjects are sketchily handled, but on the whole the work is a real contribution to medical physiology.—L. H. S.

Physiology in Health and Disease, by C. J. Wiggers, M. D. xxvii+1156 pp. Philadelphia, Lea and Febiger, 1934.

A Co-operative Discussion of Psychological Thought

A group of specialists have brought together, under the editorship of Dr. F. A. Moss, a fine discussion of modern comparative psychology. Beginning with the historical background of the subject, the chapters proceed through "instinctive" functions, incentives and drives, effects of hormones, functions of receptors, the problems of discrimination and learning, the measurement and implications of individual differences, social concepts, and special abilities. The authors have done a fine piece of team-work, and have largely overcome the usual objections to a co-operative venture in writing.—L. H. S.

Comparative Psychology, by twelve psychologists, edited by F. A. Moss. xiii+529 pp. New York, Prentice-Hall, 1934.

What is Truth?

This is one of the most stimulating books it has been the good fortune of this reviewer to read in a long time. Pilate's age-old question is subjected to a searching analysis, resulting, of course, in the conclusion that the question itself is really devoid of meaning. The steps in the process of reaching this conclusion are, however, beautifully laid out. The book is replete with sentences and paragraphs that the reader could wish to frame and keep ever before him. Many of them will remain engraved on his memory for all time to come. To all searchers after truth this book is recommended as a bright light on a dim road.—L. H. S.

The search for Truth, by Eric Temple Bell. x+279 pp. Baltimore, The Williams and Wilkins Co., 1934.

Is the World a Soulless Mechanism?

"The Great Design" presents a brilliant symposium of all the sciences written by fourteen eminent scientists who have been asked "to state in outline how the world seems to them, first as scientists and then as men." Every subject, from stars to the green leaf, has been carefully and painstakingly developed and the result is a broad survey of science which is understandable to the layman and acceptable to the most exacting of scientists.

The only fault one can find with the book is the "purpose" for which it was written. Sir J. Arthur Thomson expresses it thus: ". . . we are writing primarily for those who have not this assurance (that 'God's in His heaven, all's right with the world'), yet may be helped toward it by thinking quietly over the world which Science discovered, and by enjoying it, too."

Many of the writers are extremely scientific in the analyses of their particular fields, ignoring the whole matter of design in nature. Then they awaken to the fact (in the last paragraph of their chapter) that they must "present evidence that might seem to point to Mind or Intelligence behind nature," and they fulfill their "purpose" by quoting a poem, or an excerpt from the Bible.

The book gives intellectual satisfaction to those who are interested only in the philosophical implications of science, and scientific satisfaction to those who accept only the facts and accuracies of science and not metaphysics. Driesch, Metcalf, MacBride and the others seem to have combined the scientific and philosophical fields to their own satisfaction, but—is it Science?—H. S. HYMAN.

The Great Design, edited by Frances Mason. 324 pp. New York, The Macmillan Company, 1934.

Bibliography of Nature Study

For the use of teachers and others interested in nature study Professor Vinal has collected a bibliography of nearly two thousand titles together with their sizes, pages, publishers and prices. A loose attempt at classification of the titles has been attempted and some are indicated as especially suited for children. The list is composed entirely of titles in book form such as would appear in publishers catalogues and omits journal or magazine articles. In other words it is a book list. It might be of particular use in establishing a nature study library.

—D. F. M.

Nature Education—A Selected Bibliography, by W. G. Vinal. School of Education, Western Reserve University, Cleveland, No. 39; 82 pp. 1935. Unbound, mimeographed. Price, 75 cents.

Minerals

This handy book is divided into three parts; first, "About Minerals in General," in which in 126 pages are given the general phenomena and the various ways of handling them. The second part confines itself to the "Description of Minerals," where, in 124 pages, are described some 180 fairly common or important minerals. The third, "Description of Rocks," devotes 11 pages to handling some two dozen common rock types. Appendix I has tables for identification of minerals (33 pages). Appendix II is a Pronouncing Vocabulary, six pages with a good index at the end. For the numerous amateur mineral-collectors this is a good beginning handbook. For those who desire to know the more abundant minerals it should prove a great boon. It is not technical as are the orthodox books on minerals. On the other hand, it is not a great departure from the classic texts. For the casual student of minerals, it should prove very useful. Mr. English has produced a book which eloquently speaks for itself and which should find many users.—WILLARD BERRY.

Getting Acquainted with Minerals, by George L. English. xi+324 pp., 258 illustrations. Rochester, N. Y., Mineralogical Publishing Co., 1934.